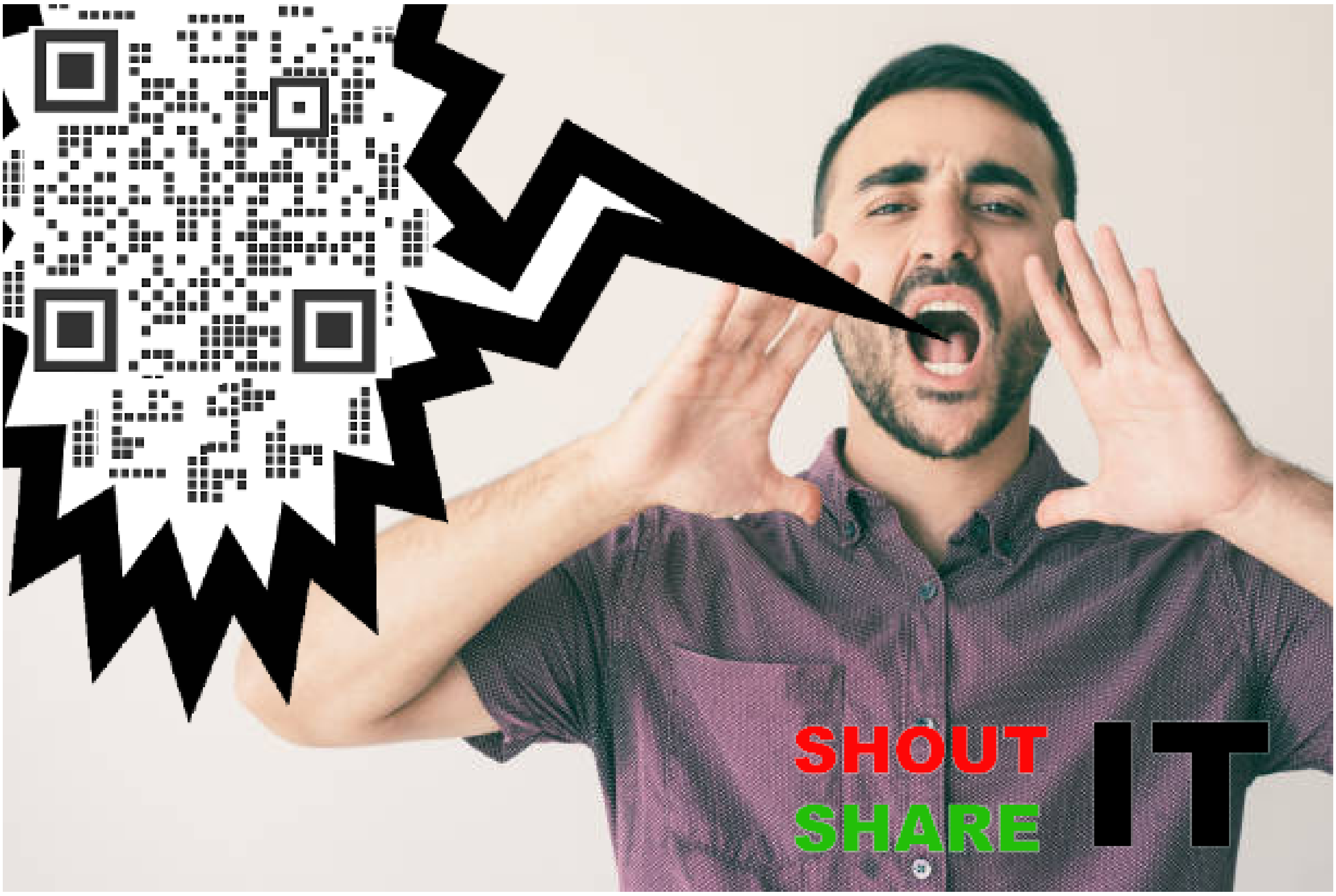
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D. J. Carter & M. B. Hart

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Aspects of mid-Cretaceous stratigraphical micropalaeontology

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Synopsis

The mid-Cretaceous foraminifera of southern England and northern France have been studied, and the diagnostic species utilized in the formulation of a zonal scheme; the taxonomy of these stratigraphically diagnostic forms is briefly discussed. The zonation has been used in a reappraisal of British mid-Cretaceous stratigraphy. An important non-sequence has been found in the mid-Cenomanian, and this feature has been related to possible changes in the palaeogeography of the North Atlantic Ocean. Two new species, *Plectina cenomana* n. sp. and *Flourensina mariae* n. sp., and one new variety, *Lingulogavelinella globosa* (Brotzen) var. *convexa* nov., are described.

Introduction

This account reviews the micropalaeontological evidence bearing on Cenomanian stratigraphy, and complements similar accounts based on ammonite palaeontology which have appeared during the last few years. In many places the occurrence of foraminifera permits correlation where ammonite evidence is lacking, and comparison of both schemes leads to a more accurate understanding of the Cenomanian Stage in Great Britain. In areas where the microfaunal and macrofaunal evidence appears to conflict, the disagreements are shown to be due to sedimentological complexity rather than faunal divergence.

It is over eighty years since A. J. Jukes-Browne and W. Hill presented their paper (1896) on 'Delimitation of the Cenomanian' to the Geological Society of London, and until recently this was the most important statement on the British mid-Cretaceous. Although Kennedy's (1969, 1970) work questions some of their theories the majority remain undisputed. Foraminiferal distribution, hitherto largely neglected in studies of British Cenomanian stratigraphy, is here used to check the validity of their proposed correlations. These are amended where necessary and the foraminiferal evidence used to relate the British sequence to the equivalent successions in Europe and North America.

Résumé of Cenomanian research

The Turonian Stage was erected in 1842 by Alcide d'Orbigny for the group of calcareous rocks found in the Touraine (France). D'Orbigny (1842 : 404) states: 'Je propose de désigner à l'avant l'étage qui m'occupe (craie chloritée, glauconie crayeuse, craie tuffeau, et grès verts) sous le nom Turonien, de la ville de Tours (Turones) ou de la Touraine (Turonia) situées sur ces terrains.'

After a study of the ammonites and rudists d'Orbigny redefined the Turonian in 1847, thereby erecting a separate stage – the Cenomanian – for the lower part of the original Turonian. Lecointre (1959) designated the Cher Valley as the type section for the redefined Turonian. However, nowhere in the Touraine can a full succession be seen in a continuous exposure, and the outcrops extend from Frétevou to Chisseaux – a distance of some 28 km – along the north side of the Cher Valley. At Frétevou the lowermost Turonian, thin-bedded marly chalk, overlies a sandy marl which in turn rests on glauconitic, oyster-bearing sands. These sands contain abundant *Exogyra columba* (d'Orbigny) and were included by d'Orbigny within the Cenomanian Stage.

The Cenomanian, therefore, was defined as the lower part of the original Turonian and the type area is regarded as the Sarth region of France. Many sections listed by d'Orbigny have been overgrown or destroyed during the last century, although several new exposures are now available. Guillier (1886) estimated that the Sarthe Cenomanian attained a thickness of 101 m, and this has been corroborated by Juignet (1968), who produced a figure of 100 m for the Cenomanian at Le Mans. In the area immediately east and north of this city the Cenomanian displays so many lateral and vertical facies variations that it is difficult to work out the succession.

Largely through poor exposure the upper levels of the Cenomanian succession are relatively little known. Where recorded their fauna consists mainly of *Ostrea* spp. and *E. columba*, neither of which prove useful for correlation. The lower levels contain a fauna largely of *Exogyra* spp. and other molluscs. These faunas are in a different facies from those of the type Albian of the Aube region of eastern France (Fig. 1) and it is not surprising that correlation difficulties have arisen. As initially defined, the Albian consisted mainly of what is now accepted as Lower Albian and there was little mention of Upper Albian faunas. This led to the erection of the 'Vraconian' Stage for the *Stoliczkaia dispar* Zone.

Between 1840 and 1870 the British Cretaceous was subdivided into lithological units, with only passing reference to the faunas. Details of this early work are summarized in Jukes-Browne & Hill (1900, 1903) and repetition is unnecessary.

Barrois' (1876) study of British Cretaceous stratigraphy used the stage names newly established in France. Many French geologists (Guillier 1886, Hébert 1857, etc.) had difficulty rationalizing d'Orbigny's standard 'stages', and Barrois' attempt at so distant a correlation was thought premature. Jukes-Browne & Hill (1896) clearly outlined their concept of the Cenomanian and this differed from that of Barrois. Barrois included nearly half the Upper Greensand within the Cenomanian Stage, while the English geologists considered the Cenomanian the exact equivalent of the Lower Chalk. In England it had just been accepted that the Gault Clay and the Upper Greensand were lateral equivalents and Jukes-Browne even suggested a name be found for this Gault Clay/Upper Greensand 'Stage' (eventually called the Selbornian). Jukes-Browne & Hill (1896), commenting on the work of Barrois, stated:

'The result of British investigations, therefore, has been to tell us that our subdivisions into Gault, Upper Greensand and Lower Chalk do not tally in any way with their Albien and Cenomanien stages and that if we wished to adopt the French nomenclature we should have to draw a hard and fast line in the middle of the Upper Greensand.

'The work of English geologists has therefore tended to consolidate the Gault and Upper Greensand, and to separate them as a whole from the overlying Lower Chalk, which has generally a bed of glauconitic marl at its base, and is often marked off from the Upper Greensand by a very clear plane of division. The faunal assemblages agree with this method of classification and no modern English geologist would imagine that a more natural division could be made by grouping a part of the Upper Greensand with the Lower Chalk.'

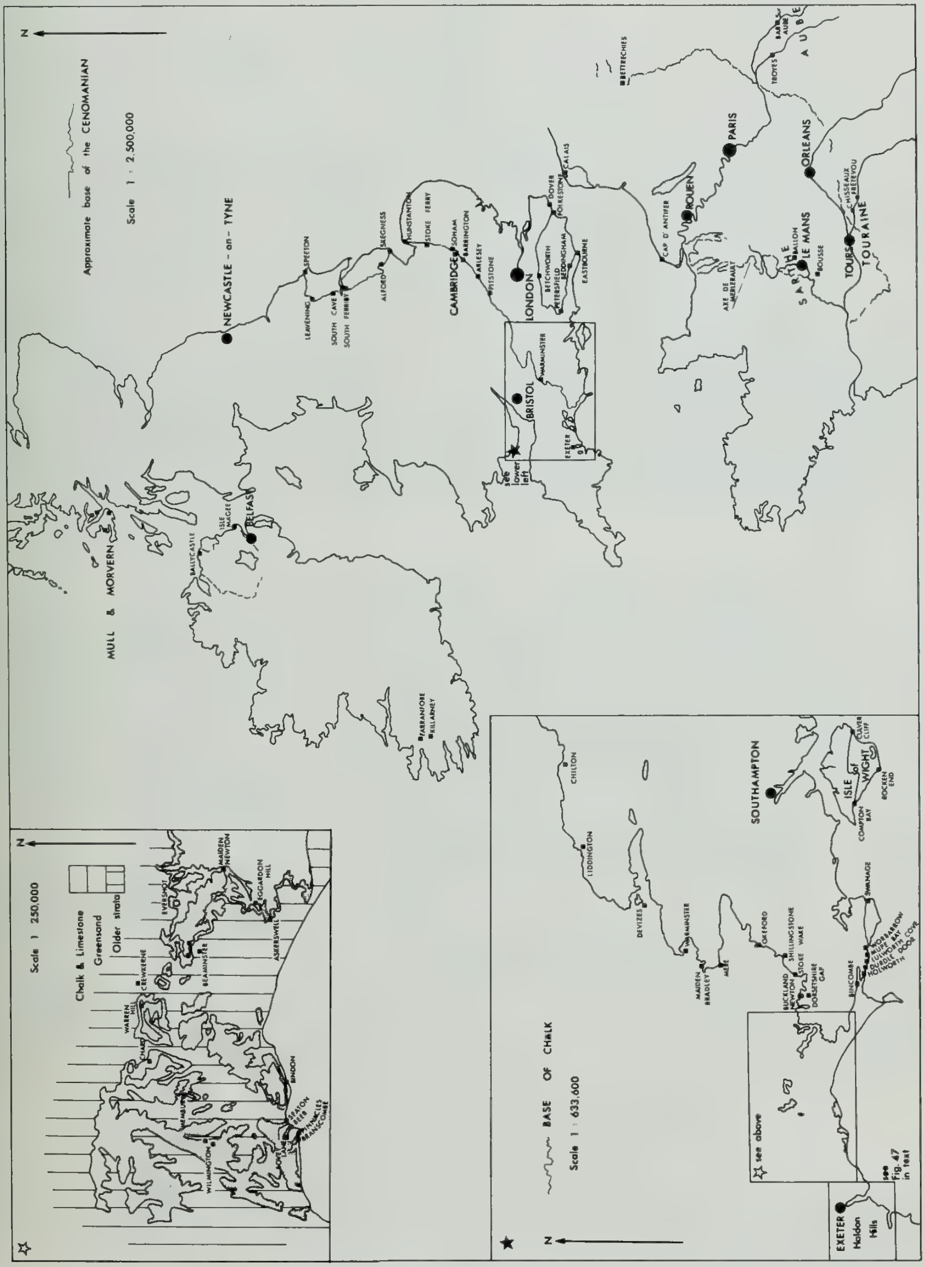
N
Approximate base of the CENOMANIAN
Scale 1 : 2,500,000
NEWCASTLE - on - TYNE
SPEETON
LEAVENING
SOUTH CAVE
SOUTH FERRIBY
ALFORD
SKEGNESS
HUNSTANTON
STOKE FERRY
SOHAM
BARRINGTON
CAMBRIDGE
ARLESEY
PITSTONE
LONDON
BETCHWORTH
PETERSFIELD
BEDDINGHAM
EASTBOURNE
DOVER
FOLKESTONE
CALAIS
BRISTOL
WARMINSTER
EXETER
see lower left
MULL & MORVERN
ISLE MAGEE
BELFAST
BALLYCASTLE
FARRANFORE
KILLARNEY
BETTRECHIES
PARIS
ROUEN
CAP D' ANTIFER
AXE DE MERLERAULT
SARTHE
BALLON
LE MANS
BOUSSE
ORLEANS
TOURS
TOURAINE
CHISSEAUX
FRETEVOU
TROYES
BAR-S-AUBE
AUBE
Scale 1 : 250,000
Chalk & Limestone
Greensand
Older strata
MAIDEN NEWTON
EGGARDON HILL
EYPESMOUTH
ASKERSWELL
BEAMINSTER
CREWKERNE
WARREN HILL
CHARD
BINDON
BEER
SEATON
BRANSCOMBE
WIMBLEDON
WILMINGTON
BASE OF CHALK
Scale 1 : 633,600
CHILTON
LIDDINGTON
DEVIZES
WARMINSTER
MAIDEN BRADLEY
MERE
OKEFORD
SHILLINGSTONE
STOKE WAKE
BUCKLAND NEWTON
DORSETSHIRE GAP
BINCOMBE
SOUTHAMPTON
ISLE of WIGHT
CULVER CLIFF
ROCKEN END
COMPTON BAY
SWANAGE
WORBARROW
MUPE BAY
LULWORTH COVE
DURDLE DOOR
HOLWORTH
see above
see Fig. 47 in text
EXETER
Haldon Hills

Fig. 1 Locality map of the Anglo-Paris Basin. Inset, western areas of Cretaceous outcrop in more detail.

Since 1896 the lithostratigraphic terms of the English geologists and the chronostratigraphic terms of the French often have appeared side-by-side and both have been much misused. Only sporadic attempts at clarification have been made since 1900. The major contribution of Jukes-Browne & Hill was a series of memoirs on the 'Cretaceous Rocks of Britain' (1900–1904). Their ideas and conclusions are the basis for all later research and only recently have they been critically examined. These books still contain the most complete account yet produced of the British Cretaceous. Spath (1926, 1923–43) and Wright & Wright (1949) produced ammonite zonations for the Albian and Cenomanian. Although the Gault Clay is suitable for such studies the Upper Greensand is not and our knowledge of it has remained largely as it was in Jukes-Browne's time. Smith (1957a, etc.) continued the work of Meyer (1874) in south-west England, and provided very detailed accounts of that rather isolated area of Cretaceous sediments. Unfortunately these marginal deposits were not correlated precisely with the more normal successions of south-east England.

In 1962–63 Jefferies produced two works on the micropalaeontology and stratigraphy of the *Actinocamax plenus* Marls. These showed the advantages of studying a small part of the succession in detail. They demonstrated that apparently uniform chalk may display marked microfaunal changes through quite small stratigraphic thicknesses, and it was partly this approach that inspired the mode of the present research. They permitted tight correlations of the Plenus Marls and its use as a reference datum. Other workers in recent years, e.g. Tresise (1960), persisted in using the base of the Lower Chalk as a datum, even after Wright (*in* Arkell 1947) had demonstrated that the base of the Lower Chalk becomes younger towards the south-west of England. However, Jeans (1968), who showed that a series of pulse faunas can be recognized in the Lower Chalk, based his clay mineral distribution diagrams on plotted sections using the Plenus Marls as datum.

The last major works were those of Kennedy (1969, 1970), on the ammonite faunas. His studies primarily were of assemblages and, while these have aided our understanding of the Cenomanian, the authors still feel that much of the stratigraphy of the south-west of England remains to be explained. Using both the ammonites and the microfaunas the authors hope to correlate the marginal facies more accurately.

Mid-Cretaceous foraminifera: Systematics

The total foraminiferal population of the mid-Cretaceous includes well over five hundred species. While many of these are stratigraphically useful only a limited number are of major significance. All the species used in the proposed zonation occur in large numbers, and a sample taken from any stratigraphic level would yield the described diagnostic fauna. The only exception is *Conorboides lamplughi* (Sherlock) – the marker for Gault Clay Zone 3 – which can be a little difficult to find unless a large amount of material is processed. These diagnostic species are used in a zonal scheme based on assemblages characteristic of restricted stratigraphic intervals.

The classification of the Foraminiferida has been discussed in detail and the majority of previous classifications analysed by Loeblich & Tappan (1964, *Treatise*). Their classification has been accepted by the majority of micropalaeontologists. The present authors have deviated from it in only a few places, and these are documented. This report primarily is of stratigraphic interest and not intended as a detailed account of foraminiferal taxonomy.

All type and figured specimens, together with some unfigured material, are deposited in the British Museum (Natural History), London, registered numbers P 49941 – P 50040 inclusive.

Order **FORAMINIFERIDA** Eichwald 1830

Suborder **TEXTULARIINA** Delage & Hérouard 1896

Superfamily **LITUOLACEA** de Blainville 1825

Family **ATAXOPHRAGMIIDAE** Schwager 1877

In recent years many workers have become dissatisfied with Loeblich & Tappan's (1964) classification of this family. For a fuller report – particularly regarding *Arenobulimina* Cushman – see

Loeblich & Tappan (1961a) and Gawor-Biedowa (1969). Loeblich & Tappan's classification of the genera considered in this account is as follows:

Subfamily Verneuilininae: *Flourensina* Marie, *Gaudryina* d'Orbigny, *Tritaxia* Reuss.
Subfamily Globotextulariinae: *Arenobulimina* Cushman, *Dorothia* Plummer, *Eggerellina* Marie.
Subfamily Valvulininae: *Plectina* Marsson.
Subfamily Ataxophragmiinae: internally subdivided '*Arenobulimina*' referred to *Ataxophragmium* Reuss or *Hagenowina* Loeblich & Tappan.

Loeblich & Tappan followed Trujillo (1960 : 308) in placing *Marssonella* Cushman in the synonymy of *Dorothia* Plummer. In the present work *Marssonella* has been reinstated. They rejected Bowen's (1955 : 363) theory that *Gaudryina* d'Orbigny, *Dorothia* and *Marssonella* are congeneric. Although rejection is confirmed here, it must be emphasized that these genera are closely related. A suprageneric classification that divides these three between two subfamilies is quite artificial; we place *Dorothia* and *Marssonella* with *Gaudryina* in the Subfamily Verneuilininae. *Plectina* Marsson is also quite closely related to *Dorothia*, differing only in the terminal position of the aperture. While Loeblich & Tappan state that *Plectina* displays a well-developed valvular tooth, no British specimens have been seen showing this feature. The illustration of *Plectina ruthenica* Reuss given by Loeblich & Tappan does not resemble the type figure and this variance is borne out by subsequent references. Until the type specimens have been re-examined, *Plectina* should be included in the *Gaudryina*, *Dorothia* and *Marssonella* group, i.e. the Subfamily Verneuilininae.

Arguments for changing the classificatory position of *Arenobulimina* have been presented by Gawor-Biedowa (1969). The most important observation is that both *Arenobulimina* Cushman and *Ataxophragmium* Reuss can have either simple or complex interiors and, as they are very similar in both shape and apertural characteristics, it is illogical to place them in different subfamilies. The Subfamily Globotextulariinae therefore has been rejected, and the genus *Arenobulimina* placed in the Subfamily Ataxophragmiinae. It must be emphasized that a complete revision of the Family Ataxophragmiidae is needed. This should include a full analysis of all the available type material.

The provisional reclassification is therefore as follows:

Subfamily Verneuilininae: *Dorothia* Plummer, *Flourensina* Marie, *Gaudryina* d'Orbigny, *Marssonella* Cushman, *Plectina* Marsson, *Tritaxia* Reuss.
Subfamily Ataxophragmiinae: *Arenobulimina* Cushman, *Eggerellina* Marie.

Subfamily **VERNEUILININAE** Cushman 1911

Genus ***DOROTHIA*** Plummer 1931

TYPE SPECIES. *Gaudryina bulletta* Carsey 1926.

Dorothia filiformis (Berthelin 1880)
(Plate 1, fig. 3)

1880 *Gaudryina filiformis* Berthelin: 25; pl. 1, fig. 8.
1892 *Gaudryina filiformis* Berthelin; Chapman: 752; pl. 11, fig. 7.

REMARKS. This very thin biserial species usually can be recognized by its small size and almost parallel sides.

RANGE. Middle and Upper Albian, Zones 3–5a; rare with a scattered distribution in Zone 6.

Genus ***FLOURENSINA*** Marie 1938

TYPE SPECIES. *Flourensina douvillei* Marie 1938.

Flourensina intermedia ten Dam 1950
(Fig. 2)

1950 *Flourensina intermedia* ten Dam: 15; pl. 1, fig. 16.

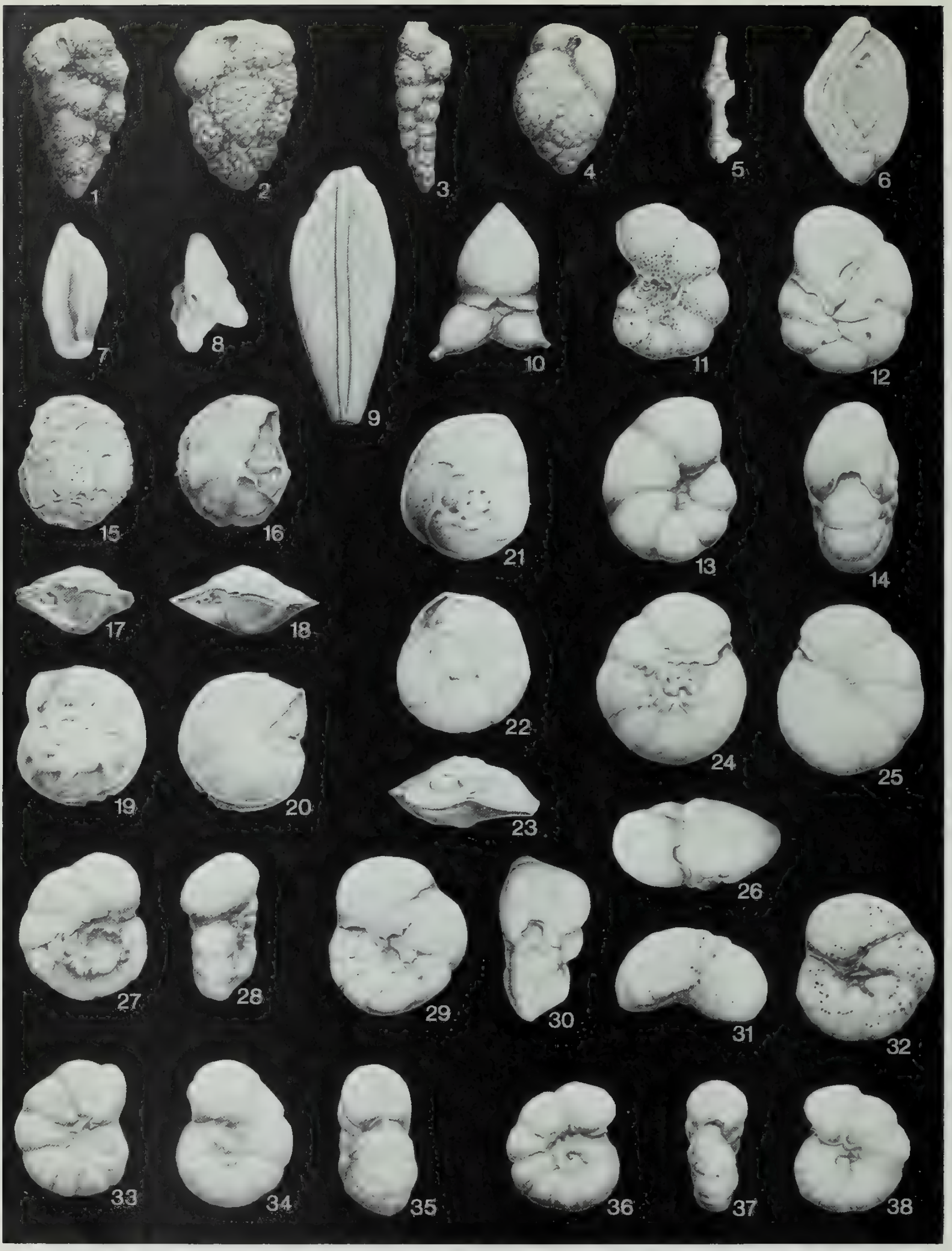
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Plate 1

Fig. 1 *Arenobulimina frankei* Cushman. P 49944. Side view. Upper Albian Zone 6, Bed XIII, East Wear Bay, Folkestone, Kent. × 38. (See also Pl. 2, fig. 5.)

Fig. 2 *Arenobulimina sabulosa* (Chapman). P. 49949. Side view. Upper Albian Zone 6, Bed XIII, East Wear Bay, Folkestone, Kent. × 32.

REMARKS. This distinctive triserial species appears fully developed in Zone 6a, and very small, rare, atypical specimens have been found in the lower part of Zone 5a. It has not been recorded farther north than Barrington, Cambridgeshire. The most westerly occurrence is at Beddingham (Sussex). Some badly-preserved specimens of *Flourensina* somewhat similar to this species have been recorded from the sections on the Isle of Wight.

RANGE. Lower Cenomanian chalk and greensand, Zones 6a–8.

Flourensina mariae sp. nov.
(Plate 2, fig. 6)

DERIVATION OF NAME. This species has been named after P. Marie, in recognition of his work on the genus *Flourensina*.

DIAGNOSIS. A *Flourensina* with a loop-shaped aperture, which projects up from the basal suture. The species is characterized by the irregular outline of the later chambers, caused by infolding of the chamber margins.

DESCRIPTION. Test free, agglutinated, coarse-grained, and rough externally; triserial throughout, but chamber arrangement in the late growth stages obscured by the coarse agglutination of the final whorl. Chambers increasing rapidly in size, the last-formed whorl occupying approximately

Fig. 3 *Dorothia filiformis* (Berthelin). P 49950. Side view. Middle Albian Zone 4, Bed IV, Copt Point, Folkestone, Kent. ×91.

Fig. 4 *Arenobulimina chapmani* Cushman. P 49951. Side view. Upper Albian Zone 6, Bed XIII, East Wear Bay, Folkestone, Kent. ×34.

Fig. 5 *Nodobacularia nodulosa* (Chapman). P 49952. Side view. Upper Albian Zone 5, Bed XI, Copt Point, Folkestone, Kent. ×32.

Fig. 6 *Spiroloculina papyracea* Burrows, Sherborn & Bailey. P 49953. Upper Albian Zone 6, Bed XIII, East Wear Bay, Folkestone, Kent. ×39.

Figs 7, 8 *Quinqueloculina antiqua* (Franke). P 49954–5. Side and apertural views. Lower Cenomanian Zone 8, Barrington, Cambridgeshire. Fig. 7, ×32; Fig. 8, ×40.

Fig. 9 *Citharinella pinnaeformis* (Chapman). P 49958. Side view. Upper Albian Zone 5, Bed XI, Copt Point, Folkestone, Kent. ×14.

Fig. 10 *Schackoina cenomana* (Schacko). P 49959. Side view. Middle Cenomanian Zone 11(ii), Ackers Steps, Dover, Kent. ×141.

Fig. 11 *Globigerinelloides bentonensis* (Morrow). Specimen lost by authors. Side view. Middle Cenomanian, Greenhorn Formation, western interior, U.S.A. – supplied by D. Eicher. ×91. (See also Pl. 2, figs 19–20.)

Figs 12–14 *Lingulogavelinella globosa* (Brotzen). P 49961. Ventral, dorsal and peripheral views. Upper Cenomanian Zone 14 (iia), Compton Bay, Isle of Wight. ×48.

Figs 15–17 *Hoeglundina carpenteri* (Reuss). P 49964. Dorsal, ventral and peripheral views. Middle Albian Zone 3, Bed III, Copt Point, Folkestone, Kent. ×38.

Figs 18–20 *Hoeglundina chapmani* (ten Dam). P 49967. Peripheral, dorsal and ventral views. Middle Albian Zone 3, Bed II, Copt Point, Folkestone, Kent. ×43.

Figs 21–23 *Conorboides lamplughi* (Sherlock). P 49970. Dorsal, ventral and peripheral views. Middle Albian Zone 3, Bed I, Copt Point, Folkestone, Kent. ×36.

Figs 24–26 *Lingulogavelinella globosa* var. *convexa* nov. P 49972. Ventral, dorsal and peripheral views. Upper Cenomanian Zone 14(i), Merstham, Surrey. ×57.

Figs 27, 28 *Gavelinella cenomanica* (Brotzen). P 49973. Ventral and peripheral views. Middle Cenomanian Zone 11(i), Compton Bay, Isle of Wight. ×32.

Figs 29, 30 *Lingulogavelinella jarzevae* (Vasilenko). P 49975. Ventral and peripheral views. Lower Cenomanian Zone 8, East Wear Bay, Folkestone, Kent. ×52.

Figs 31, 32 *Gavelinella tormarpensis* Brotzen. P 49978. Peripheral and ventral views. Middle Albian Zone 3, Bed II, Copt Point, Folkestone, Kent. ×81.

Figs 33–35 *Gavelinella intermedia* (Berthelin). P 49981. Ventral, dorsal and peripheral views. Middle Cenomanian Zone 11(ii), Culver Cliff, Isle of Wight. ×44.

Figs 36–38 *Gavelinella baltica* Brotzen. P 49984. Dorsal, peripheral and ventral views. Upper Cenomanian Zone 14(i), Merstham, Surrey. ×30.

one third of the total length of the test. Margins of the chambers in the late growth stages infolded, giving a crenulate outline to the test in apertural view, and marginal buttresses parallel to the axis of coiling present in the interior. Apertural face flattened, aperture loop-shaped, projecting upwards from the basal suture, in a slight depression.

DIMENSIONS. Holotype – overall height 1·23 mm, overall width 0·75 mm.

LOCALITY AND HORIZON. The holotype (P 49991) is from Middle Cenomanian Zone 12, Buckland Newton, Dorset.

DISTRIBUTION. This species has been found in southern England, extending only as far north as Barrington, Cambridgeshire, and as far west as mid-Dorset.

REMARKS. This Upper Cenomanian species is a late member of the *F. intermedia* lineage. The triserial growth form and the loop-shaped aperture distinguish it as a *Flourensina*, rather than a member of the quadriserial *Arenobulimina anglica* Cushman lineage. *A. anglica* superficially resembles *F. mariae* in showing crenulated chamber margins in the last whorl.

RANGE. Upper Cenomanian chalk (Zones 11(ii)–13); most abundant in Zone 12. The rare specimens found in Zone 14 in the Channel area may be derived.

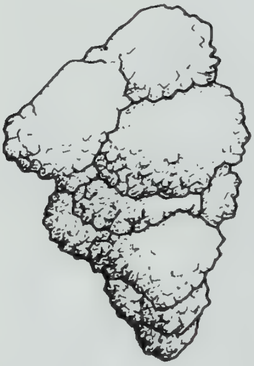


Fig. 2 *Flourensina intermedia* ten Dam. P 49941. Side view. Sample 51710, Martello Tower No. 3 section, Lower Cenomanian Zone 7, East Wear Road, Folkestone, Kent. ×39.

Comments on the *Flourensina* group

F. intermedia may develop from the *A. sabulosa* (Chapman) lineage (see Fig. 3) high in the Upper Albian by reduction from quadriserial to triserial growth form. However, no intermediate forms have been found. *F. intermedia* is triserial, but the coarse agglutination makes separation from *A. sabulosa* difficult.

F. mariae is unlike any other member of the genus in that the agglutination is not sufficiently coarse to obscure the chamber arrangement, and the outer walls of the later chambers are infolded on lines parallel to the axis of coiling producing buttresses and giving crenulate chamber margins. This infolding is a late development in the *F. intermedia* lineage. However, there is no evidence from Zones 8–11(ii) of any intermediate forms. It is unlikely that *F. mariae* is descended from the *A. anglica* lineage. Although *A. anglica* develops similar internal structures and crenulate chamber margins at the end of its range in Zones 10 and 11(i), the test remains quadriserial. It seems more likely that the formation of the crenulate chamber margins, which is always more marked than in *A. anglica*, is a parallel development.

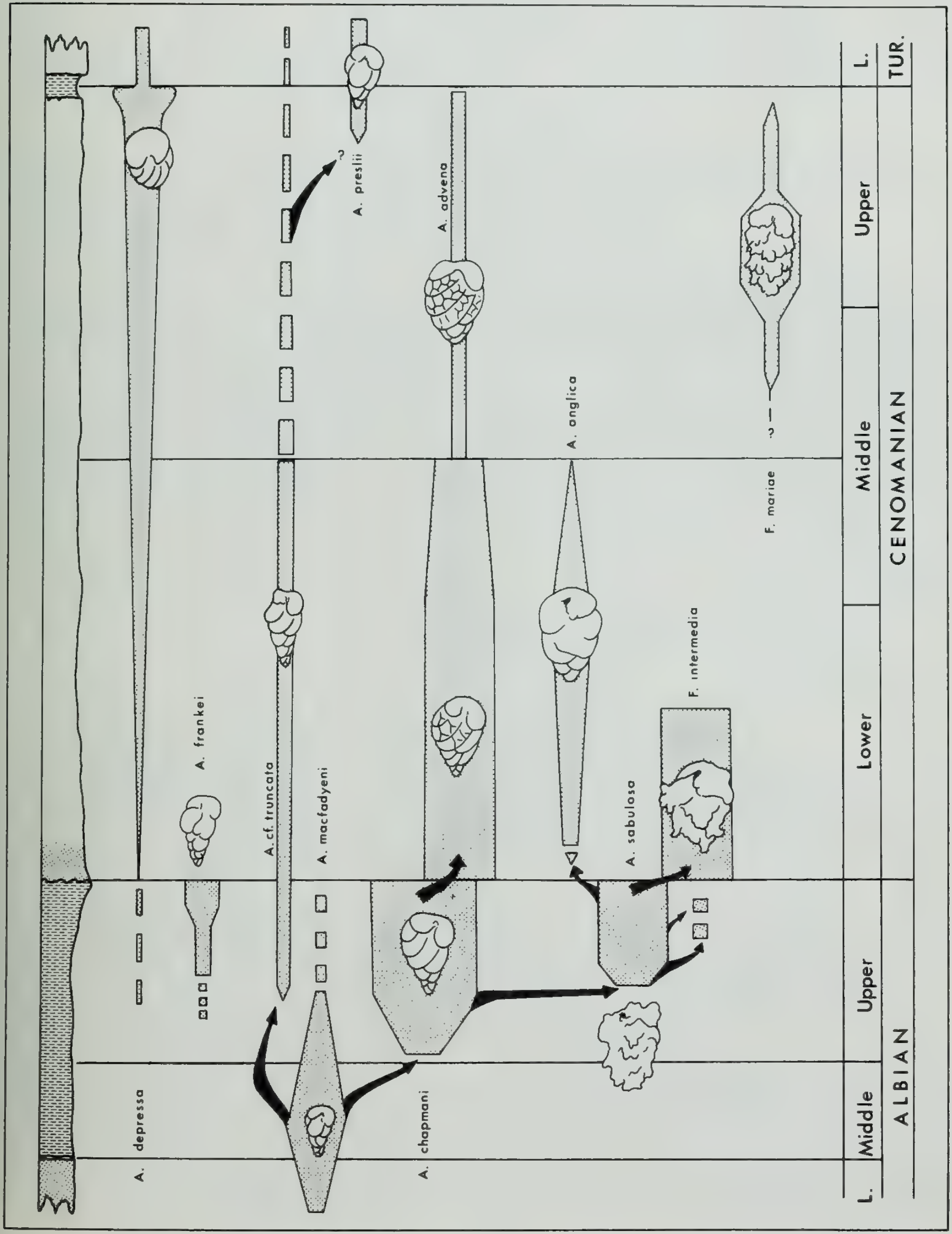
F. mariae is most abundant in Zone 12 where the associated fauna indicates a shallowing, with erosion in some areas. The development of the buttresses may have been a response to this more turbulent environment. The same level displays a significant, although temporary, reduction in the planktonic population. Although it has not been accurately placed, this level could be the boundary between the Middle Cenomanian (*Acanthoceras rotomagensis* Zone) and the Upper Cenomanian (*Calycoceras naviculare* Zone).

Genus *GAUDRYINA* d'Orbigny *in* de la Sagra 1839

TYPE SPECIES. *Gaudryina rugosa* d'Orbigny 1840.

Gaudryina austinana Cushman 1936
(Plate 2, fig. 10)

1936 *Gaudryina* (*Siphogaudryina*) *austinana* Cushman: 10; pl. 2, fig. 6a–b.
1937a *Gaudryina* (*Siphogaudryina*) *austinana* Cushman; Cushman: 74, pl. 11, figs 1–3.



A. depressa
A. frankei
A. cf. truncata
A. macfadyeni
A. preslii
?
A. chapmani
A. advena
A. anglica
A. sabulosa
F. intermedia
F. mariae
?
L.
Middle
Upper
ALBIAN
Lower
Middle
Upper
CENOMANIAN
L.
TUR.

Fig. 3 Evolution of the *Flourensina* and *Arenobulimina* groups.

1944 *Gaudryina* (*Siphogaudryina*) *austinana* Cushman; Cushman & Deaderick: 53; pl. 9, figs 15–16
1946 *Gaudryina* (*Siphogaudryina*) *austinana* Cushman; Cushman: 35; pl. 8, figs 5–7.
1954 *Gaudryina* (*Siphogaudryina*) *austinana* Cushman; Frizzell: 71; pl. 5, fig. 23a–b.
1962 *Siphogaudryina* sp. Jefferies: pl. 78, fig. 21a–b.

Remarks. Although the specimens found in the British Cenomanian are smaller than the types, it is probable that they belong to this species. The characteristic triserial growth stage makes recognition easy, although several specimens have been found in which it is much reduced.

Although this species appears in Zone 6a it only becomes abundant in the lower levels of the Plenus Marls (Bed 1). Within the Cenomanian there are levels of greater abundance (e.g. Zone 12), where there is a suggestion of shallower water conditions.

Range. Upper Albian/Cenomanian Zone 6a to Lower Turonian, with levels of greater abundance at the Zone 11(i)/(ii) boundary and in Zones 12 and 14(iia) (Plenus Marls, Beds 2 and 3).

Genus ***MARSSONELLA*** Cushman 1933

Type species. *Gaudryina oxycona* Reuss 1860.

Marssonella ozawai Cushman 1936
(Plate 2, fig. 1)

1936 *Marssonella ozawai* Cushman: 43; pl. 4, fig. 10a–b.
1937a *Marssonella ozawai* Cushman; Cushman: 59; pl. 6, fig. 18.
1953 *Marssonella ozawai* Cushman; Barnard & Banner: 205; pl. 19, fig. 2a–b.
1963 *Marssonella ozawai* Cushman; Barnard: 41–42, text-fig. 1a–c.

Remarks. Although this species appears in the Upper Albian it is only found in large numbers in the lower levels of the Cenomanian. It can be differentiated easily from its closely related species, *M. trochus* (d'Orbigny), by its coarser agglutination and almost subparallel sides. Rare transitional forms between *M. ozawai* and *M. trochus* occur in the Upper Gault Clay of the Channel area.

Range. First appearance in Upper Albian Zone 5a; when present in abundance it is characteristic of Cenomanian Zones 7–9.

Genus ***PLECTINA*** Marsson 1878

Type species. *Gaudryina ruthenica* Reuss 1851.

Plectina cenomana sp. nov.
(Plate 2, fig. 9)

1962 *Verneuilina polystropha* (Reuss) Jefferies: pl. 78, fig. 14.

Derivation of name. This species is characteristic of the Middle and Upper Cenomanian, and has been used as an indicator of this interval in the proposed zonation.

Diagnosis. The overall triserial appearance of this species differentiates it from other members of the genus.

Description. Test free, of medium-sized agglutinated material with much calcareous cement. Small proloculus followed by two or three trochospiral whorls with up to five chambers in each whorl, and usually forming less than one quarter the length of the test, remainder consisting of two to four whorls of three chambers per whorl, which in adult forms may be followed by a final pair of chambers. This arrangement gives an overall triserial appearance, and although the chambers do not increase rapidly in size the test appears to taper rapidly. Sutures distinct, depressed in the later growth stages, appearance affected by variation in the amount of cementing material. Aperture normally rounded, occasionally oval, positioned in a slight depression in the final chamber; not truly terminal but never interiomarginal, always simple with no teeth or other modifications.

The early growth stages of this species, and the appearance of its aperture, relate it to *P. mariae* (Franke).

DIMENSIONS. Holotype – overall length 0·80 mm, overall width 0·42 mm.

LOCALITY AND HORIZON. The holotype (P 49995) is from Upper Cenomanian Zone 13, Buckland Newton, Dorset.

DISTRIBUTION. This species has been recorded from the Upper Cenomanian of the whole of England (Yorkshire to Devonshire), and from northern France.

REMARKS. While rare juveniles have been seen in the Lower Cenomanian, this species is usually found in the Middle and Upper Cenomanian. In the proposed zonation it is diagnostic of Zones 11 to 13.

RANGE. Middle and Upper Cenomanian Zones 11–13. Very rare specimens have been found in Zone 14(i) (Bed 1 of the Plenus Marls).

Plectina mariae (Franke 1928)
(Plate 2, fig. 8)

1928 *Gaudryina ruthenica* Reuss var. *mariae* Franke: 146; pl. 13, fig. 15a–b.
1937b *Plectina ruthenica* (Reuss) var. *mariae* (Franke) Cushman: 106; pl. 11, fig. 15.
1948 *Plectina ruthenica* (Reuss) Williams-Mitchell: 97; pl. 8, fig. 3.
1962 *Plectina ruthenica* (Reuss); Jefferies: pl. 78, fig. 12.
1972 *Plectina ruthenica mariae* (Franke); Gawor-Biedowa: 34; pl. 3, fig. 3a–b.

REMARKS. The original specimens of *G. ruthenica* from the Senonian appear to possess a more elongate test with many more pairs of biserial chambers than those recorded from the British Isles. Franke, in establishing var. *mariae* for forms with fewer biserial chambers, recorded specimens more closely related to those we have found in our work. Even Franke's specimen, with five pairs of biserial chambers, has more than its British counterparts, which show only three or four. This difference does not warrant specific differentiation. *P. mariae* has not been recorded above the Cenomanian, and as there is no direct link between *mariae* and *ruthenica* both names are retained.

RANGE. Appearing in the basal Cenomanian (Zone 7) this species persists to the top of Bed 1 of the Plenus Marls (Zone 14(i)).

Genus ***TRITAXIA*** Reuss 1860

TYPE SPECIES. *Textularia tricarinata* Reuss 1844.

Tritaxia pyramidata Reuss 1862
(Plate 2, fig. 15)

1862 *Tritaxia pyramidata* Reuss: 32, 88; pl. 1, fig. 8a–c.
1892 *Verneuilina triquetra* Chapman: 329; pl. 6, fig. 24a–b (*non* Münster).
1892 *Tritaxia tricarinata* Chapman: 749–750; pl. 1, fig. 1a–b (*non* Reuss).
1925 *Tritaxia pyramidata* Reuss; Franke: 18; pl. 2, fig. 1a–c.
1928 *Tritaxia pyramidata* Reuss; Franke: 138; pl. 12, fig. 18a–c.
1931 *Tritaxia pyramidata* Reuss; Plummer: 133; pl. 10, figs 18–20.
1937a *Tritaxia pyramidata* Reuss; Cushman: 22–23; pl. 2, figs 21–24; pl. 3, figs 1–8.
1950 *Tritaxia pyramidata* Reuss; ten Dam: 12–13.
1953 *Tritaxia pyramidata* Reuss; Barnard & Banner: 195; pl. 7, fig. 1a–b, text-figs 5J–N.
1957 *Tritaxia pyramidata* Reuss; Vaptsarova: 45; pl. 2, fig. 3.
1959 *Tritaxia pyramidata* Reuss; Maslakova: 92; pl. 1, fig. 7.
1961 *Tritaxia pyramidata* Reuss; Akimez: 83–84; pl. 3, figs 1a–b, 2.
1962 *Tritaxia tricarinata* (Reuss) var. *pyramidata* Reuss; Jefferies: pl. 78, fig. 3.
1965 *Tritaxia pyramidata* Reuss; Neagu: 5; pl. 1, figs 9–10.
1965 *Tritaxia tricarinata* Reuss; Neagu: 6; pl. 1, figs 7–8, 17–18.
1972 *Tritaxia pyramidata* Reuss; Gawor-Biedowa: 27–28; pl. 1, fig. 10a–b.

REMARKS. This species is characteristic of the Cenomanian (Zones 7–13) and is found in flood abundance in the lower levels of this interval (Zones 7–10). It has not yet been recorded above Bed 3 of the Plenus Marls, although there are Turonian records in the literature. The full range may have to be extended down to Zone 3 of the Middle Albian, although the specimens from these levels are not completely typical of the species as a whole. The chamber arrangement and aperture are identical with those of forms from the Cenomanian but the agglutination is coarser. Jefferies (1962) illustrated three distinct species of *Tritaxia* from the Plenus Marls as varieties of *T. tricarinata* (var. *plummerae* Cushman, var. *pyramidata* Reuss and var. *macfadyeni* Cushman) but did not differentiate between them in his plots (text-figs 6–11). Specimens from Bed 4 and above belong in his '*T. tricarinata* var. *macfadyeni*', =*T. tricarinata* Reuss s.s.

RANGE. Middle Albian (Zone 3) to Bed 3 of the Plenus Marls (Zone 14(iia)).

Subfamily ***ATAXOPHRAGMIINAE*** Schwager 1877

Genus ***ARENOBULIMINA*** Cushman 1927

TYPE SPECIES. *Bulimina preslii* Reuss 1846.

Arenobulimina advena (Cushman 1936)

(Plate 2, fig. 4)

1936 *Hagenowella advena* Cushman: 43; pl. 6, fig. 21a–b.
1937b *Hagenowella advena* Cushman; Cushman: 174; pl. 21, figs 3a–b, 4.
1945 *Hagenowella advena* Cushman; Brotzen: 44–45; pl. 1, fig. 3.
1961 *Hagenowella chapmani* (Cushman); Vasilenko: 22–23; pl. 3, fig. 3a–b; not pl. 4, figs 2a–b, w, 3.
1962 *Hagenowella advena* Cushman; Jefferies: pl. 78, fig. 13.
1969 *Arenobulimina advena* (Cushman) Gawor-Biedowa: 86–90; pl. 8, figs 1–4, text-figs 7, 8.

REMARKS. Brotzen (1945) regards Cushman's statement that the type specimens (of Upper Senonian age) were from 'Junz, near Commin, Pommerania, Germany', was erroneous, and suggests that the actual locality must have been 'Zunz, near Kammin, Pommerania'. The beds at this locality are Upper Cenomanian (Brotzen 1942), and in agreement with our recorded distribution.

Although externally almost identical with *A. chapmani* Cushman, this species can easily be identified by the complex pattern of internal marginal partitions developed in the later chambers. On the external surface the partitions appear as light and dark bands, and can also be studied by breaking the specimens, or treatment with very weak acid. There is complete transition between this species and *A. chapmani* at or about the Albian-Cenomanian boundary within Zone 6a, and this appears to be unaffected by facies changes. Throughout the Cenomanian there is a transition from forms with relatively simple internal partitions to those with a complex pattern of small chamberlets, and from a study of the type of internal subdivision the position of any specimen within the Cenomanian sequence can be roughly estimated.

The overall shape of the test is very variable and ranges from long and thin to short and round. Shape differences may be because two generations are present. Close examination has shown that the long, slender specimens are microspheric.

RANGE. Upper Albian/Lower Cenomanian (Zone 6a) to Upper Cenomanian Zone 14(i) (Plenus Marls Bed 1). This species is most abundant in the Lower Cenomanian Zones 7–10.

Arenobulimina anglica Cushman 1936

(Plate 2, fig. 3)

1936 *Arenobulimina anglica* Cushman: 27; pl. 4, fig. 8a–b.
1937b *Arenobulimina anglica* Cushman; Cushman: 37; pl. 4, figs 31, ?32, not 33, 34.
1947 *Arenobulimina anglica* Cushman; Grekoff: 2; pl. 1, fig. 5a–b.

REMARKS. This species was initially described from the Chalk Marl detritus of Charing, Kent, and the holotype is typical of specimens found in the lower part of the Chalk Marl sequence. However, Cushman's (1937b) paratype (fig. 32) is very like *A. obliqua* (d'Orbigny) and the other specimen (fig. 33) is internally subdivided and should be included in *A. advena*. Although the holotype shows no sign of internal subdivisions, specimens from higher levels of the Chalk Marl (Zone 10) show a slight folding of the margins of the later chambers, similar to that already described in *F. mariae*.

RANGE. Lower Cenomanian Zones 8–11(i), although rare specimens have been found in Zones 7 and 11(ii). Specimens apparently transitional to *A. sabulosa* occur in Zone 6a.

Arenobulimina chapmani Cushman 1936
(Plate 1, fig. 4)

1892 *Bulimina preslii* Chapman: 755; pl. 12, fig. 4 (*non* Reuss).
1936 *Arenobulimina chapmani* Cushman: 26; pl. 4, fig. 7a–b.
1937b *Arenobulimina chapmani* Cushman; Cushman: 36; pl. 3, figs 27–28.
1947 *Arenobulimina chapmani* Cushman; Grekoff: 493; pl. 1, fig. 1a–b.
1950 *Arenobulimina chapmani* Cushman; ten Dam: 14.
1955 *Arenobulimina preslii* (Reuss) 1851 et aff. sp.; Bettenstaedt & Wicher: 503; pl. 4, fig. 29.
1962 *Arenobulimina preslii* (Reuss); Bartenstein & Bettenstaedt: 290; pl. 41, fig. 5; text-fig. 18.
1965 *Arenobulimina chapmani* Cushman; Neagu: 10; pl. 2, fig. 9.
1969 *Arenobulimina chapmani* Cushman; Gawor-Biedowa: 81–84; pl. 5, figs 1a–b, 2; pl. 7, figs 1a–b, 2; text-figs 3, 4.

REMARKS. This species is remarkable for its almost total lack of variation. The only significant difference is in the number of chambers in the final whorl of mature specimens – four in the lower and five in higher zones. *A. chapmani* was first recorded by Chapman from Beds VI–XIII of the Gault Clay sequence at Copt Point, Folkestone. In areas where Zone 6a is wanting there is a very marked change in the population between Zones 6 and 7 – the latter containing forms with internal partitions, placed in *A. advena*. Where Zone 6a is present there is a transition between the two species.

RANGE. Albian Zones 4a–6a.

Arenobulimina frankei Cushman 1936
(Plate 1, fig. 1; Plate 2, fig. 5)

1936 *Arenobulimina frankei* Cushman: 27; pl. 4, fig. 5a–b.
1937b *Arenobulimina frankei* Cushman; Cushman: 37–38; pl. 4, fig. 21a–b.
1947 *Arenobulimina frankei* Cushman; Grekoff: 494; pl. 1, fig. 2a–b.
1957 *Arenobulimina frankei* Cushman; Mikhailova-Jovtheva: 103; pl. 1, fig. 14a–b.
1969 *Arenobulimina frankei* Cushman; Gawor-Biedowa: 84–86; pl. 5, figs 4, 5; pl. 7, figs 6, 7a–b, 8a–b; text-figs 5, 6.

REMARKS. This species has an almost triangular, 'wedge-shaped' test, which is uniformly triserial throughout all the growth stages. *A. frankei*, initially described from the Cenomanian of Hildesheim (now Mierczany, Poland), was almost twice the size of the British specimens, although they are probably conspecific. Gawor-Biedowa gave the range in Poland as Upper Albian and Cenomanian with a size variation that would include the British specimens. Her comparative material comes from the same region as Cushman's.

RANGE. Rare juveniles appear in the lower part of Upper Albian Zone 6 but large numbers are found only in its upper levels. It persists into Zone 6a but is only found near the base.

Arenobulimina macfadyeni Cushman 1936
(Plate 2, fig. 2)

1892 *Bulimina orbignyi* Chapman: 754; pl. 12, fig. 2 (*non* Reuss).
1936 *Arenobulimina macfadyeni* Cushman: 26; pl. 4, fig. 6a–c.
1937b *Arenobulimina macfadyeni* Cushman; Cushman: 35; pl. 4, figs 13, 14.
1950 *Arenobulimina macfadyeni* Cushman; ten Dam: 14.
1965 *Arenobulimina macfadyeni* Cushman; Neagu: 10; pl. 2, figs 7, 8.
1967 *Arenobulimina macfadyeni* Cushman; Uguzzoni & Radrizzani: 1201; pl. 88, figs 7, 8.

REMARKS. This small species is common in the Lower Gault Clay (Middle Albian), and at its maximum development in Beds VII–VIII. In the Upper Albian occasional specimens are found which are much larger and which possess more coarsely agglutinated tests. These are thought to be later members of the same group.

RANGE. While this species is recorded from the Middle Albian Zones 3, 4 and 4a, it has also been found in the Lower Greensand, and its earliest occurrence cannot be placed accurately. Although specimens have been found from higher levels in the Albian they are atypical and have not been used in the zonation.

Arenobulimina sabulosa (Chapman 1892)
(Plate 1, fig. 2)

1892 *Bulimina preslii* Reuss var. *sabulosa* Chapman: 755; pl. 12, fig. 5.
1934 *Arenobulimina sabulosa* (Chapman) Cushman & Parker: 32; pl. 6, fig. 6a–b.
1937b *Arenobulimina sabulosa* (Chapman); Cushman: 36; pl. 3, figs 29, 30.
1947 *Arenobulimina sabulosa* (Chapman); Grekoff: 499; pl. 2, fig. 3a–b.
1957 *Verneuilinoides borealis* Tappan; Tappan: 206; pl. 66, fig. 16, not figs 10–15, 17–18.
1967 *Arenobulimina sabulosa* (Chapman); Kaptarenko-Chernousova: 74; pl. 14, fig. 2a–b.
1969 *Arenobulimina sabulosa* (Chapman); Gawor-Biedowa: 77–80; pl. 5, fig. 3; pl. 7, fig. 3a–b; text-figs 1–2.

REMARKS. Chapman (1898, Appendix 3) states that this form is restricted to Beds XII and XIII of the Copt Point succession. In the USSR (Dnieper – Don depression) there are records of Cenomanian occurrences, as well as Albian to Cenomanian records for the central Volga region. The range of Upper Albian to Cenomanian has also been recorded from Poland. In Britain there is no evidence that this species persists into the Cenomanian, although redeposited specimens may occur at the base, in Zone 7. This quadriserial species is usually easily recognized, although an increase in the coarseness of the agglutination can cause some confusion with *F. intermedia* ten Dam.

RANGE. Upper Albian Zones 5a and 6; Upper Albian/Lower Cenomanian Zone 6a.

Comments on the *Arenobulimina* group

A. macfadyeni is the only member of the *Arenobulimina* plexus in the basal Gault Clay (Middle Albian). Throughout the Middle Albian there is very little change in this species apart from a slight increase in size of the adult specimens. At, or about, the Middle/Upper Albian boundary at Folkestone diversification of the group begins, see Fig. 3, p. 11. The two new species appearing at this level give very little indication of their origin, although it is probable that one, the numerically important *A. chapmani*, developed from the *A. macfadyeni* lineage. The origin of *A. frankei* is uncertain, and it is possible that this species does not belong in the *Arenobulimina* plexus. It has a very restricted range, and while primitive forms are recorded from Upper Albian Zone 5, it is otherwise confined to Upper Albian Zone 6. In Zone 6a it evolves into the typically Cenomanian *Plectina mariae*. *A. chapmani* is ancestral to the majority of the Cenomanian species and is also dominant in the Upper Albian. In the uppermost Albian some very coarsely agglutinated specimens are found, while others increase steadily in size. This is the first sign of the separation into the two lineages seen in the lower levels of the Cenomanian. The *A. chapmani* group continues across the Albian/Cenomanian boundary with little, if any, change in external morphology. However, there are marked internal differences. Those from the Cenomanian are always seen to have developed a complex pattern of internal structures, typical of the species *A. advena*. This transition from *A. chapmani* to *A. advena* is always observed at the Albian/Cenomanian boundary irrespective of facies. In the basal Cenomanian these internal structures are essentially simple, marginal partitions, but at higher levels more and more complex modifications appear. The progression is not steady, as examples of the simpler forms occur at all levels within the Cenomanian. In the lower levels of the Plenus Marls (Zone 14(i), Bed 1) all variations from the very simple to the highly complex forms occur. The internally subdivided forms then disappear suddenly and do not persist into the Turonian.

Those specimens of *A. chapmani* that develop a much coarser test in the upper levels of the Albian gradually alter their chamber arrangement until they are referable to the typically quadriserial species *A. sabulosa*. This is recorded from Upper Albian Zones 5a, 6 and 6a. Others become triserial and, near the top of Zone 5a, give rise to the first, small, rare specimens of *Flourensina intermedia*. Just below the Cenomanian boundary *A. sabulosa* gives rise to *A. anglica*, through the intermediate forms seen in Zone 6a.

Small, rounded forms which show no apparent relationship to any of the above-mentioned species are present throughout the whole of the Albian and Cenomanian. Although they are thought to represent immature, megalospheric individuals of one or more of the above groups, no direct relationship can be proved. No attempt has been made to assign any of these forms to particular species as they appear to be of no stratigraphic value.

Genus *EGGERELLINA* Marie 1941

TYPE SPECIES. *Bulimina brevis* d'Orbigny 1840.

Eggerellina mariae ten Dam 1950
(Plate 2, fig. 7)

1950 *Eggerellina mariae* ten Dam: 15–16; pl. 1, fig. 17.
1962 *Eggerellina* sp. Jefferies: pl. 79, fig. 5.
1972 *Eggerellina mariae* ten Dam; Gawor-Biedowa: 33–34; pl. 3, figs 1a–b, 2a–b.

REMARKS. This is a very variable species and completely accurate references are almost impossible without further study. The external shape varies from short pyramidal to long and narrow. It is probable that this species is ancestral to *E. intermedia* (Reuss), which is commonly recorded from higher levels in the Cretaceous.

At certain levels within the Cenomanian, particularly in the lower horizons of the Plenus Marls, there are several varieties of *Eggerellina* present in almost every sample. On morphology alone these could be placed in several 'species' and varieties (*E. brevis* (d'Orbigny) var. *conica* Marie, *E. murchisoniana* (d'Orbigny), *E.* cf. *E. puschi* (Reuss), etc.). In our opinion these are intergrading variants of a single plexus which begins with *E. mariae* in the Albian and leads to *E. intermedia* in the Senonian. Other generic groups develop numerous variants in the Plenus Marls and we suggest that the extreme variation seen at this level is ecophenotypic.

RANGE. This species appears in the uppermost levels of Zone 5 (Upper Albian), becomes abundant in Zone 5a, and continues in varying numbers throughout the Cenomanian into the Lower Turonian.

Family **ORBITOLINIDAE** Martin 1890

Genus *ORBITOLINA* d'Orbigny 1850

TYPE SPECIES. *Orbitolites lenticulata* Lamarck 1816, =*Madreporites lenticularis* Blumenbach 1805.

Orbitolina lenticularis (Blumenbach 1805)

1805 *Madreporites lenticularis* Blumenbach: pl. 80, figs 1–6.
1816 *Orbulites concava* Lamarck: 197.
1816 *Orbulites lenticulata* Lamarck: 197.
1850 *Orbitolina lenticulata* (Lamarck) d'Orbigny: 143, no. 342.
1850 *Orbitolina concava* (Lamarck) d'Orbigny: 185, no. 745.
1900 *Orbitolina concava* (Lamarck); Egger: 145; pl. 22, fig. 34; pl. 24, figs 38–40; pl. 26, figs 1–18.
1948 *Orbitolina* cf. *concava* (Lamarck); Henson: 61; pl. 4, figs 5–10; text-fig. 10j–r.
1960 *Orbitolina concava* (Lamarck); Douglass: 32; pls 2, 3.
1963 *Orbitolina lenticularis* (Blumenbach); Hofker: 181–302, figs 1–24, charts 1–9, pls 1–23, and full synonymy.

REMARKS. *Orbitolina* has been recorded from strata of Barremian to Cenomanian age in the Tethyan Province, although its range in other parts of the world is somewhat shorter. The first 'Linnaean' name applied to the group was *Madreporites lenticularis* Blumenbach (1805). This was followed in principle by later workers, although various generic names (*Orbulites* Lamarck, *Orbitolites* d'Archiac) have been proposed. The genus *Orbitolina* was established in 1850 by d'Orbigny, and this name is used in preference to the earlier generic names for reasons given by Hofker (1963) and Loeblich & Tappan (1964). The early work on the differentiation of species within the genus was based on external characteristics (height, diameter, etc.). Douvillé (1904) was the first to propose the use of internal characters for taxonomic work, and this was done by

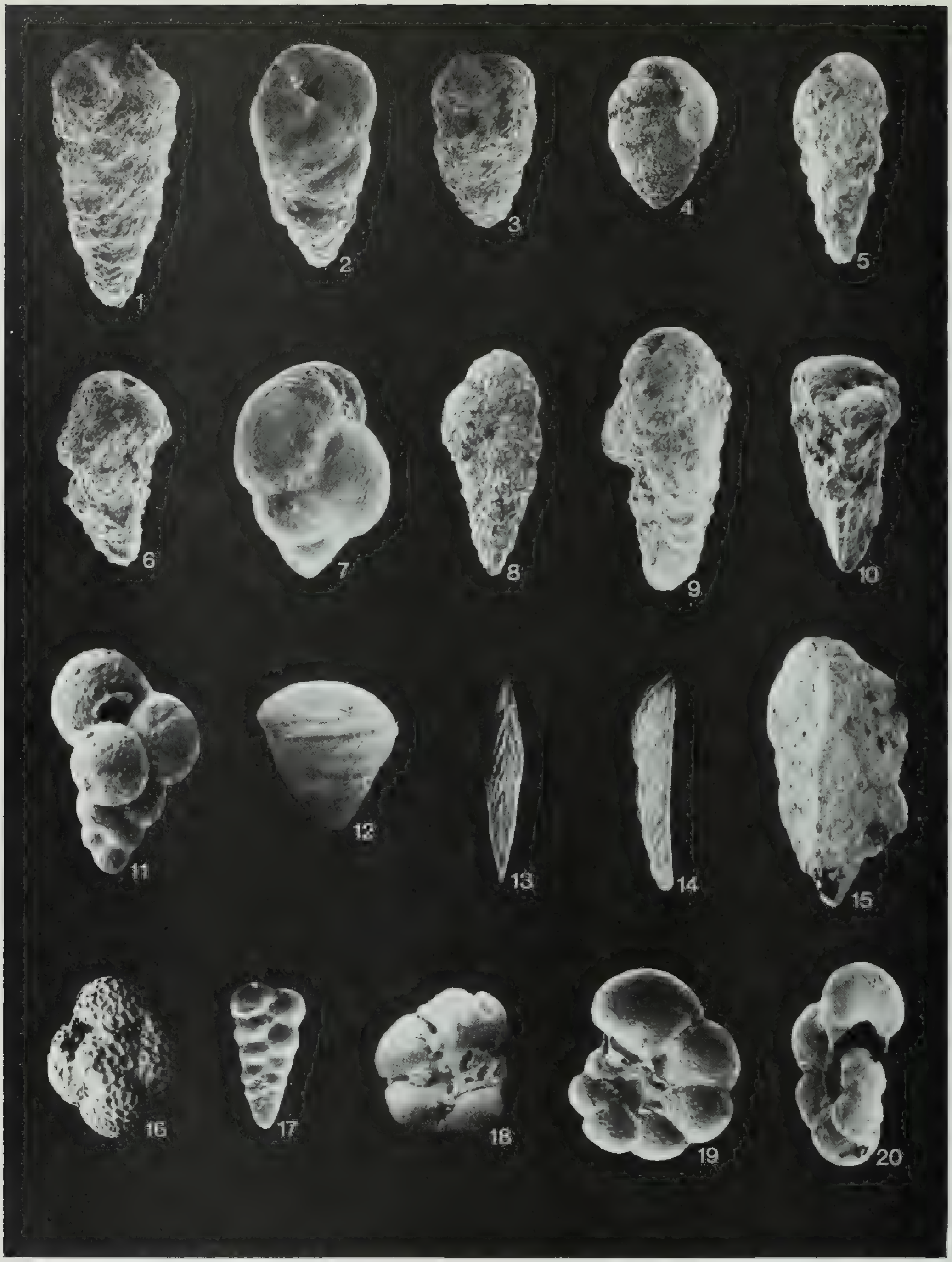

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Plate 2

Fig. 1 *Marssonella ozawai* Cushman. P 49987. Side view. Lower Cenomanian Zone 8, East Wear Bay, Folkestone, Kent. × 48.

Fig. 2 *Arenobulimina macfadyeni* Cushman. P 49988. Side view. Middle Albian Zone 3, Bed I, Copt Point, Folkestone, Kent. × 51.

Henson (1948), Douglass (1960), Ayala-Castanares (1960) and Schroeder (1962). Hofker (1963) proposed the complete subdivision of the genus into 'form groups' on the basis of the megalospheric embryonic apparatus.

The detailed account of the morphology provided by Hofker (1963) is so complete that very little can be added. However, the particular 'form group' to which the British specimens can be assigned is discussed in detail, since the location of its position in the stratigraphic sequence is important in this research. Hofker recognized that it is only the intial chambers of the megalospheric individuals that give any indication of the correct placing of specimens within the basic evolutionary sequence. This is the only part of the test which remains unaffected by ecological conditions, since it alone develops within the protective protoplasm of the microspheric generation. Henson (1948 : 71), on the basis of faunas from the Middle East, was the first to propose that the majority of populations belonged 'to a single "plexus of descent" within which we have been able to recognise certain morphological "species" and "varieties" . . .'. However, the populations are not recognized by sharply-defined characteristics and can be isolated only when considering statistical analysis of dimensions and other characters. As Henson and most later workers have found, this causes difficulties in the determination of the lower and upper limits of each 'species' and 'variety'. Hofker formulated the most extreme theory and proposed that the genus is best regarded as being monospecific; this view we uphold. The synonymy provided here

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Fig. 3 *Arenobulimina anglica* Cushman. P 49989. Side view. Middle Cenomanian Zone 10, Barrington, Cambridgeshire. × 24.

Fig. 4 *Arenobulimina advena* (Cushman). P 49990. Side view. Lower Cenomanian Zone 8, Barrington, Cambridgeshire. × 23.

Fig. 5 *Arenobulimina frankei* Cushman. P 49944. Side view. Upper Albian Zone 6, Bed XIII, East Wear Bay, Folkestone, Kent. × 43. (See also Pl. 1, fig. 1.)

Fig. 6 *Flourensina mariae* sp. nov. P 49991. Side view. Holotype, Middle Cenomanian Zone 12, Buckland Newton, Dorset. × 23.

Fig. 7 *Eggerellina mariae* ten Dam. P 49993. Side view. Upper Albian Zone 6, Bed XIII, East Wear Bay, Folkestone, Kent. × 51.

Fig. 8 *Plectina mariae* (Franke). P 49994. Side view. Lower Cenomanian Zone 8, Barrington, Cambridgeshire. × 47.

Fig. 9 *Plectina cenomana* sp. nov. P 49995. Side view. **Holotype**, Upper Cenomanian Zone 13, Buckland Newton, Dorset. × 49.

Fig. 10 *Gaudryina austinana* Cushman. P 49996. Side view, Upper Cenomanian Zone 13, Buckland Newton, Dorset. × 45.

Fig. 11 *Guembelitria harrisi* Tappan. P 49997. Side view. Upper Albian Zone 6A, Cheriton, Folkestone, Kent. × 224.

Fig. 12 *Pseudotextulariella cretosa* (Cushman). P 49998. Side view. Middle Cenomanian Zone 10, Beachy Head, Eastbourne, Sussex. × 30.

Fig. 13 *Citharinella laffittei* Marie. P 49999. Side view. Upper Albian Zone 6A, Cheriton, Folkestone, Kent. × 12.

Fig. 14 *Vaginulina mediocarinata* ten Dam. P 50000. Side view. Upper Albian Zone 5, Bed XI, Copt Point, Folkestone, Kent. × 12.

Fig. 15 *Tritaxia pyramidata* Reuss. P 50001. Side view. Lower Cenomanian Zone 8, Barrington, Cambridgeshire. × 45.

Fig. 16 *Hedbergella washitensis* (Carsey). P 50002. Dorsal view. Middle Cenomanian Zone 11(ii), *Orbirhynchia mantelliana* band, Ackers Steps, Dover, Kent. × 48.

Fig. 17 *Heterohelix moremani* (Cushman). P 50003. Side view. Upper Albian Zone 6A, Cheriton, Folkestone, Kent. × 98.

Fig. 18 *Rotalipora cushmani* (Morrow). Specimen lost by authors. Ventral view. Middle Cenomanian Zone 10/11(i), Cenomanian Sands, Bovey Lane Sandpit, Beer, near Seaton, Devon. Glauconitic cast extracted from the calcareous sandstone with dilute acid. × 30. (See also Pl. 4, figs 7–9.)

Figs 19, 20 *Globigerinelloides bentonensis* (Morrow). Fig. 19, P 50004. Side view. Upper Albian Zone 6, Gault immediately below the Cambridge Greensand, Arlesley, Cambridgeshire – topotype level of *G. caseyi* (Bolli, Loeblich & Tappan). × 109. Fig. 20, P 50005. Peripheral view. Middle Cenomanian Greenhorn Formation, western interior, U.S.A. – supplied by D. Eicher. × 117. (See also Pl. 1, fig. 11.)

only covers those references that relate to the British specimens. In all previous accounts specimens have been referred to the species *Orbitolina concava* (Lamarck).

The form groups of Hofker are distributed as follows:

Form group I	U. Barremian – U. Aptian
Form group II	U. Aptian – L. Albian
Form group III	L. Albian – U. Albian
Form group IV	U. Albian – U. Cenomanian
Form group V	U. Cenomanian

As groups III–V are found elsewhere in the stratigraphic interval under consideration a short description of each (based mainly on Hofker's work) is given here. These demonstrate, as will be shown in detail later, that the British specimens from the Upper Greensand are completely contained within group IV.

Form group III. Proloculus with flat, sometimes concave, distal wall; well-developed epiembryonic chambers with an increasing number of partitions which seldom reach the wall of the proloculus.

Form group IV. Proloculus very close in appearance to a rounded triangle; epiembryonic chambers complex and subdivided into small, interconnected cellules; height of the cellule layer generally about half the height of the deuteroconch.

Form group V. Proloculus nearly spherical or arched; outer wall of deuteroconch radial, causing the embryonic apparatus to be more or less globular.

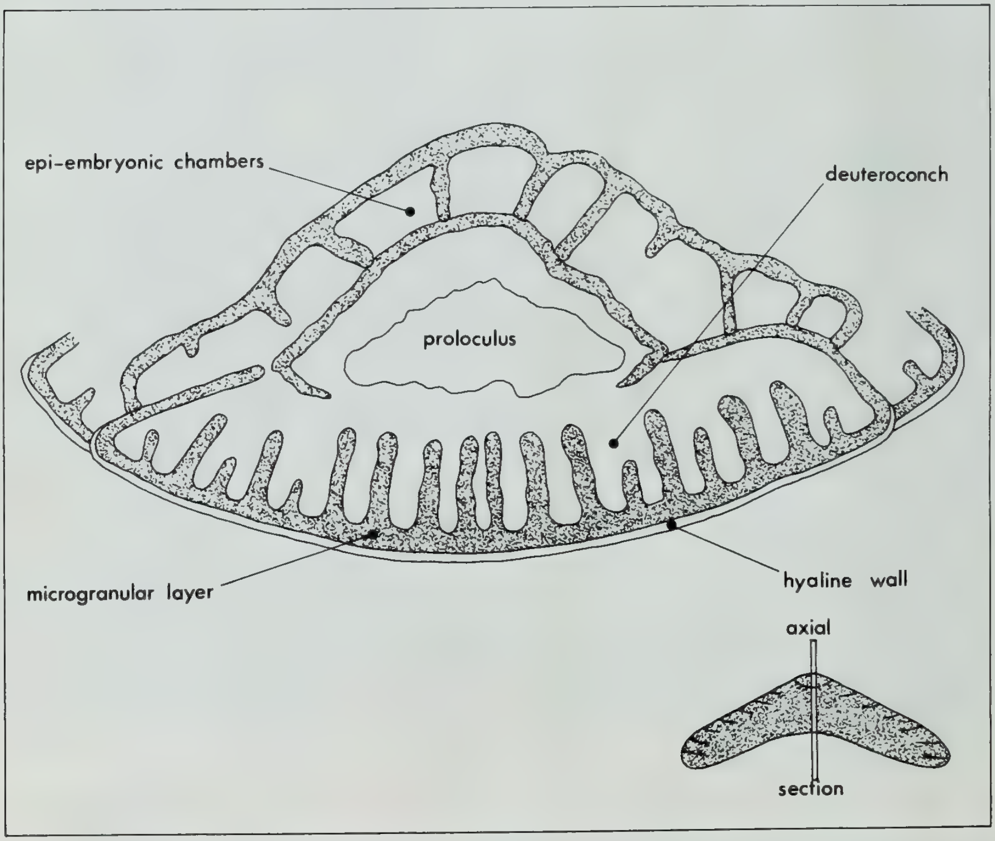

Fig. 4 Megalospheric embryonic apparatus of *Orbitolina lenticularis* (Blumenbach). Diagram built up from serial sections through a single test. (× 150.)

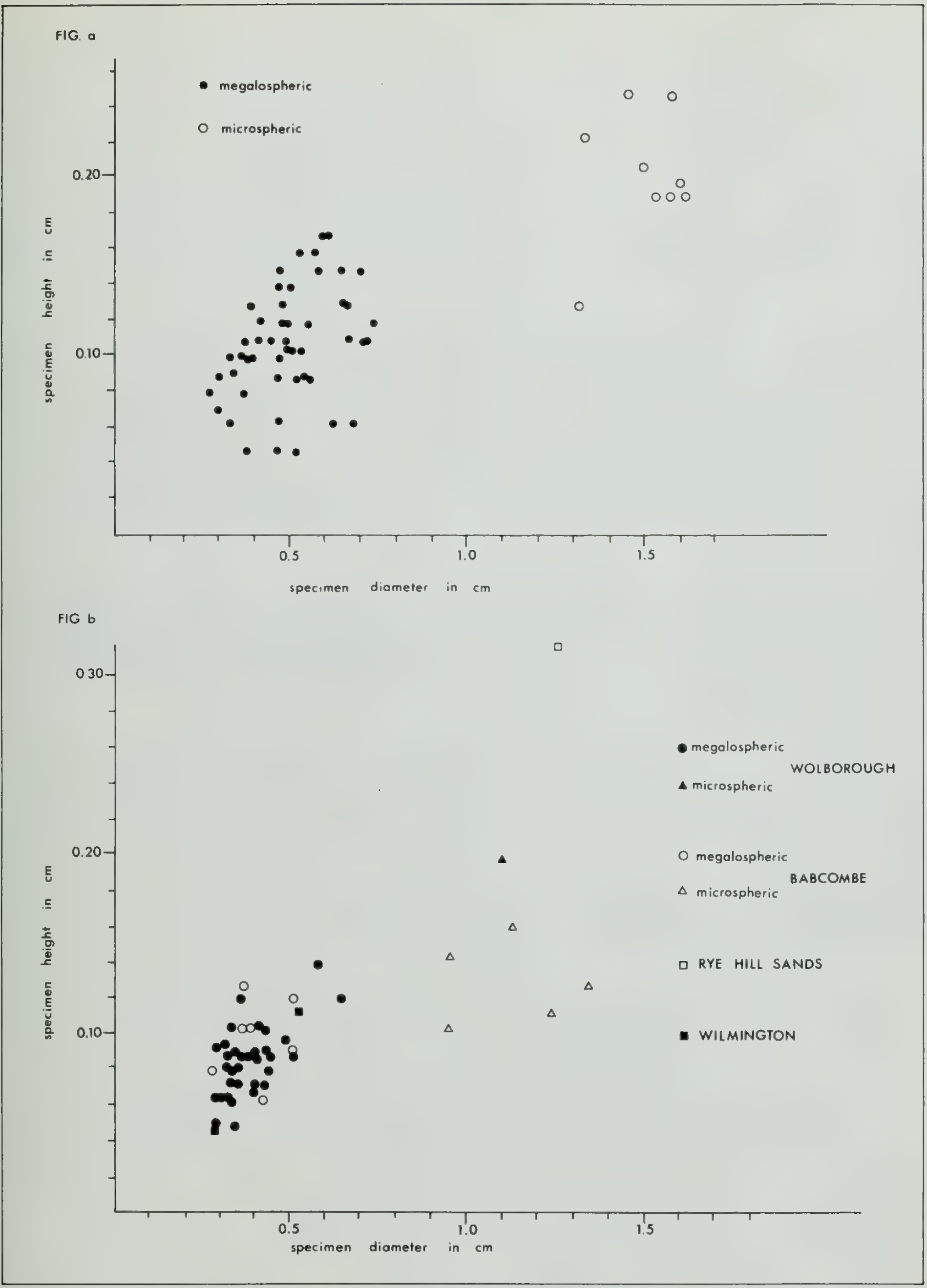

Fig. 5 Specimen height/width plots of representative populations of *O. lenticularis* (Blumenbach), (a) from Ballon, Sarthe, France, and (b) from various named localities in south-west England.

Form group IV is characterized by the species *O. concava* from the type locality of Ballon (Sarthe), France. Material from this area has been used in all comparative work and this is important in the subsequent stratigraphic analysis.

As the overall external appearance of the genus has been shown to be of little diagnostic value, the bulk of our work was done on oriented thin sections. Those which clearly showed the megalospheric embryonic apparatus provided the numerical data used in this work. The pattern of development of the embryonic apparatus was found to be almost identical to that figured by Hofker (1963 : fig. 20) as the typical form for the whole of group IV. The details of this are reproduced in diagrammatic form in Fig. 4. Using the serial sections it has been possible to establish that this form of embryonic apparatus is the only one represented in the typical Lower Cenomanian material from Ballon, and the Upper Greensand material from south-west England. It is hoped that the following data may establish that the populations in northern France and southern England were essentially synchronous, and can be used as such in any stratigraphical reinterpretation. Two comparative techniques have been used with some success.

i. Height/width ratios. While outer dimensions have proved to be of little use for taxonomic work they can be used for the comparison of two populations within one taxon. The results of this investigation are plotted in Fig. 5. The measurements immediately separate the two generations. In the Ballon assemblage of megalospheric forms there is a wider range of size variation than in those from south-west England, although the main concentration of readings from the two areas fall very close to one another. While every attempt was made to obtain perfect axial sections, this was not always achieved, and the resulting inaccuracy could account for any discrepancies.

The microspheric population from Ballon falls into a moderately restricted area of the field. The single reading at its lower margin is probably of an immature specimen. However, in the specimens from south-west England there is a tremendous range of variation between specimens from different localities. The value recorded for the single microspheric specimen from Wolborough (Devon) is nearest to the concentration recorded from Ballon, and this would be expected since the two environments would appear, on sedimentological grounds, to be very similar. The plots for the specimens from Babcombe, which generally are much flatter in appearance than those from Ballon, fall within a restricted area. However, accurate measurement of the rather decomposed specimens from Babcombe is difficult. The single specimen from the Warminster Greensand is completely unlike any other specimen recorded in this present work and the difference is probably ecophenotypic.

The data suggest that the smaller megalospheric forms are less affected by the environment than the larger microspheric ones. This may explain the comparative closeness of the two megalospheric populations and yet the wide separation of the microspheric ones.

ii. Measurements of the megalospheric embryonic apparatus. The height and width of the megalospheric embryonic apparatus (Fig. 6), when seen in axial section, have provided a second method of comparison of the two populations. In this case there is much less agreement between the two groups. There is a very wide scatter in the specimens from Ballon, and this great variation in the size and form of the embryonic apparatus was also noted by Hofker, who gave an indication of it in some of his figures. This wider variation corresponds very well with that in the overall dimensions of the same specimens. In the case of Wolborough specimens, where the overall dimensions fell within closer limits, there is more evidence of concentration. An exception to this is the single measured specimen from Babcombe where the values fit closely with the specimens from Ballon. It seems that although the populations from Ballon and Wolborough can be compared fairly closely, there are variations probably produced by differences of environment.

The environmental relationships of *Orbitolina* have been discussed by Rat (1959) and Douglass (1960). The genus occurs in most facies, although it is generally associated with clastic sediments. Douglass concluded that in most cases the evidence indicated normal salinity, in a shallow-water, marine environment. The most limiting factor was temperature, the majority of occurrences being tropical or subtropical. The occurrences in south-west England are from the highest

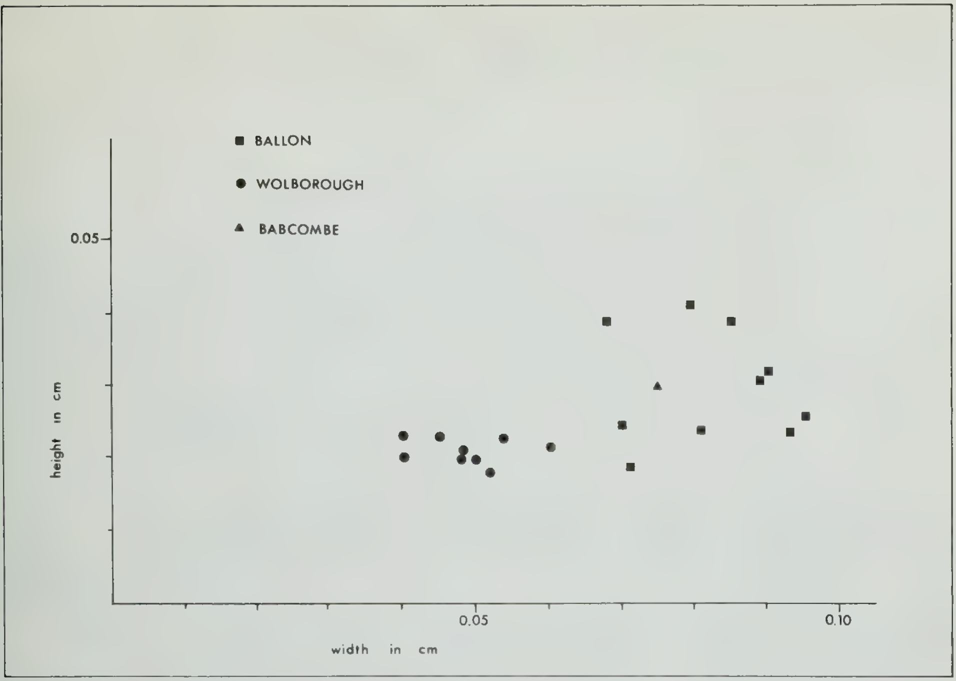

Fig. 6 Height/width plot for the megalospheric embryonic apparatus of *O. lenticularis* (Blumenbach), based on specimens from all localities. Precise axial sections are difficult to obtain; only the most reliable measurements have been used.

latitude recorded by Douglass (1960 : fig. 1), even allowing for continental movements. However, the fauna from this area is sparse, even when compared with that of northern France, and it is interesting that *Orbitolina* has not been found in south-east England. In this case the controlling factor appears to be lithofacies or depth, rather than temperature.

The *O. lenticularis* populations of south-west England are thought to belong to the same faunal community as those of the type Lower Cenomanian of the Sarthe. The occurrence of this species in the Upper Greensand of south-west England is indicative of a Lower Cenomanian age for these sediments. This statement will be expanded more fully in the stratigraphic analysis.

RANGE. Lower Cenomanian (*Mantelliceras mantelli* Zone), Zones 7–9.

Family **PAVONITINIDAE** Loeblich & Tappan 1961

Subfamily **PFENDERININAE** Smout & Sugden 1962

Genus ***PSEUDOTEXTULARIELLA*** Barnard *in* Barnard & Banner 1953

TYPE SPECIES. *Textulariella cretosa* Cushman 1932.

Pseudotextulariella cretosa (Cushman 1932)
(Plate 2, fig. 12)

1932 *Textulariella cretosa* Cushman: 97; pl. 11, figs 17–19.
1937b *Textulariella cretosa* Cushman; Cushman: 61; pl. 6, figs 26–28.
1948 *Textulariella cretosa* Cushman; Williams-Mitchell: 97; pl. 8, fig. 1.
1953 *Pseudotextulariella cretosa* (Cushman) Barnard *in* Barnard & Banner: 198; text-figs 6b–i.
1963 *Pseudotextulariella cretosa* (Cushman); Barnard: 48; pl. 7, figs 1–6; text-figs 6a–d, 7a–f, 8a–c.
1972 *Pseudotextulariella cretosa* (Cushman); Gawor-Biedowa: 34–35; pl. 3, fig. 4a–b.

REMARKS. This large, highly distinctive species occurs in large numbers in the lower levels of the Cenomanian. Barnard (1963 : text-fig. 9) indicated, quite erroneously, that this species first appears in the uppermost levels of the Albian.

RANGE. Cenomanian Zones 9–12.

Suborder **MILIOLINA** Delage & Hérouard 1896

Superfamily **MILIOLACEA** Ehrenberg 1838b

Family **NUBECULARIIDAE** Jones 1875

Subfamily **SPIROLOCULININAE** Wiesner 1920

Genus ***SPIROLOCULINA*** d'Orbigny 1826

TYPE SPECIES. *Spiroloculina depressa* Cushman 1917.

Spiroloculina papyracea Burrows, Sherborn & Bailey 1890

(Plate 1, fig. 6)

1890 *Spiroloculina papyracea* Burrows, Sherborn & Bailey: 551; pl. 8, fig. 1.
1950 *Spiroloculina papyracea* Burrows, Sherborn & Bailey; ten Dam: 18; pl. 1, fig. 19.
1967 *Spiroloculina papyracea* Burrows, Sherborn & Bailey; Fuchs: 277; pl. 5, fig. 8.

REMARKS. Although the majority of workers have referred this species to the genus *Spiroloculina*, there is some doubt about this attribution. Specimens show a minute, early, quinqueloculine growth form, which indicates a close relationship to the genus *Massilina* Schlumberger. In the present account, however, *Spiroloculina* is retained.

S. papyracea was initially described from the Albian, and all other records of the species refer to this level. Reuss (1854) also described as *S. cretacea* a species which is very similar to Burrows, Sherborn & Bailey's *S. papyracea*. However, *S. cretacea* was initially described from the Turonian to Coniacian of the Gosau area (Austria), and the subsequent references to it come only from the Upper Cretaceous. Franke (1928) referred Cenomanian specimens to *S. cretacea* and it is possible that the two species will prove synonymous. The reason for retaining *S. papyracea* is that the authors' specimens compare well with type-level material, and the specimens from the Cenomanian are identical with those from the Albian.

RANGE. This species is encountered between the Upper Albian Zone 5 and the upper levels of Cenomanian Zone 11(i), although rare specimens have been found in Albian Zone 4a and Cenomanian Zones 11(ii), 13, and 14(i–iia) (Plenus Marls Beds 1–3).

Subfamily **NODOBACULARIINAE** Cushman 1927

Genus ***NODOBACULARIA*** Rhumbler 1895

TYPE SPECIES. *Nubecularia tibia* Jones & Parker 1860.

Nodobacularia nodulosa (Chapman 1891)

(Plate 1, fig. 5)

1891 *Nubecularia nodulosa* Chapman: 573; pl. 9, fig. 2.
1948a *Nubeculina nodulosa* (Chapman) ten Dam: 177.
1949 *Pseudonubeculina nodulosa* (Chapman) Bartenstein & Brand: 670; figs 3–5.
1950 *Pseudonubeculina nodulosa* (Chapman); ten Dam: 18; pl. 1, fig. 20.
1951 *Pseudonubeculina nodulosa* (Chapman); Bartenstein & Brand: 278; pl. 4, figs 82–84.
1965 *Pseudonubeculina nodulosa* (Chapman); Neagu: 10; pl. 2, figs 25, 26.
1967 *Nodobacularia nodulosa* (Chapman) Fuchs: 278; pl. 5, figs 1, 2.

REMARKS. We have followed Fuchs (1967) in placing this distinctive species in the genus *Nodobacularia* (after Loeblich & Tappan 1964, *Treatise*).

RANGE. Albian Zones 4 and 5a, with rare and scattered specimens being found in Zone 6.

Family **MILIOLIDAE** Ehrenberg 1838b
Subfamily **QUINQUELOCULININAE** Cushman 1917
Genus ***QUINQUELOCULINA*** d'Orbigny 1826

TYPE SPECIES. *Serpula seminulum* Linné 1758.

Quinqueloculina antiqua (Franke 1928)
(Plate 1, figs 7, 8)

1891 *Miliolina venusta* Karrer; Chapman: 9; pl. 9, figs 5, 6.
1891 *Miliolina Ferussacii* (d'Orbigny); Chapman: 10; pl. 9, fig. 8.
1891 *Miliolina tricarinata* (d'Orbigny); Chapman: 10; pl. 9, fig. 9.
1928 *Miliolina* (*Quinqueloculina*) *antiqua* Franke: 126; pl. 11, fig. 26.
1950 *Quinqueloculina antiqua* (Franke) ten Dam: 17; pl. 1, fig. 18.
1954 *Quinqueloculina antiqua* (Franke); Vasilenko: 33–34; pl. 6, figs 8a, b, w, 9a, b, w.
1957 *Quinqueloculina kochi* (Reuss); Hofker: 436, text-fig. 494.
1965 *Pseudosigmoilina antiqua* (Franke) Bartenstein: 351–2.
1967 *Quinqueloculina antiqua* (Franke); Fuchs: 279; pl. 5, fig. 5a–b.
1972 *Quinqueloculina antiqua* (Franke); Gawor-Biedowa: 35–36; pl. 3, fig. 6a–c.

REMARKS. According to Chapman (1891) the sharp-edged form (*M. venusta*) is superseded upwards by the round-edged form (*M. ferussacii*). In this species the angles of the test become more rounded as growth proceeds.

RANGE. Small forms appear in Albian Zone 2, although significant numbers are found only above Zone 4; it is abundant in the Cenomanian up to and including Zone 9, although small forms have been recorded in the remainder of the Cenomanian.

Suborder **ROTALIINA** Delage & Hérouard 1896
Superfamily **NODOSARIACEA** Ehrenberg 1838a
Family **NODOSARIIDAE** Ehrenberg 1838a
Subfamily **NODOSARIINAE** Ehrenberg 1838a
Genus ***CITHARINELLA*** Marie 1938

TYPE SPECIES. *Flabellina karreri* Berthelin 1880.

Citharinella laffittei Marie 1938
(Plate 2, fig. 13)

1938 *Citharinella laffittei* Marie: 101; pl. 8, fig. 3.

REMARKS. This very long, slender species has rarely been found complete, but the characteristic ornament allows an identification of even the smallest fragments.

RANGE. Only common to Zone 6a, although the full range is from Albian Zone 5a to Cenomanian Zone 8.

Citharinella pinnaeformis (Chapman 1894)
(Plate 1, fig. 9)

1894 *Frondicularia pinnaeformis* Chapman: 185; pl. 3, figs 9–11.
1938 *Citharinella pinnaeformis* (Chapman) Marie: 100; pl. 7, figs 7–9; pl. 8, figs 4–6.
1950 *Citharinella pinnaeformis* (Chapman); ten Dam: 38–39.

REMARKS. This species is an important zonal indicator in the Upper Albian (Zone 5), where it can be used with *A. chapmani* for correlation.

RANGE. Albian Zones 4a–5a; the very rare specimens that are found in Zone 6 are probably derived.

Genus *VAGINULINA* d'Orbigny 1826

TYPE SPECIES. *Nautilus legumen* Linné 1758.

Vaginulina mediocarinata ten Dam 1950
(Plate 2, fig. 14)

1894 *Vaginulina strigillata* Chapman: 423; pl. 8, figs 3–4 (*non* Reuss).
1950 *Vaginulina mediocarinata* ten Dam: 36–37; pl. 3, fig. 3.

REMARKS. Although this species has not been found outside the Gault Clay facies, it is nevertheless useful in south-east England where it occurs typically in the Upper Albian.

RANGE. Albian Zones 4a–6.

Superfamily **GLOBIGERINACEA** Carpenter, Parker & Jones 1862

Family **HETEROHELICIDAE** Cushman 1927

Subfamily **GUEMBELITRIINAE** Montanaro-Gallitelli 1957

Genus *GUEMBELITRIA* Cushman 1933

TYPE SPECIES. *Guembelitria cretacea* Cushman 1933.

Guembelitria harrisi Tappan 1940
(Plate 2, fig. 11)

1940 *Guembelitria harrisi* Tappan: 115; pl. 19, fig. 2a–b.
1967 *Guembelitria harrisi* Tappan; Pessagno: 258; pl. 48, figs 12, 13.
1970 *Guembelitria harrisi* Tappan; Eicher & Worstell: 296; pl. 8, figs 1–2.

REMARKS. Bandy (1967) records only two species of *Guembelitria* – *G. cretacea* Cushman from the Maastrichtian and *G. harrisi* from the Albian. *G. harrisi*, the larger species, has a lower aperture, is less rapidly flaring and comparatively narrow. Bandy (1967) derives *G. cretacea* from *Heterohelix globulosa* (Ehrenberg) and it is possible that, in a similar way, *G. harrisi* is a triserial derivative of *H. moremani* (Cushman). However, it is more likely that *G. cretacea* is a continuation of the *G. harrisi* lineage, as the specimens found in the Upper Cenomanian and Lower Turonian are very similar to both *harrisi* and *cretacea*. Keller (1935) describes a species *Guembilitria cenomana* (1935 : 547; pl. 2, figs 13, 14) which is very close to *G. harrisi* Tappan.

G. harrisi differs from the *G. cenomana* of Gawor-Biedowa (1972 : 61) in the sudden increase in size of the chambers with growth, but her figure (1972 : pl. 5, fig. 4) seems to fall within the allowable range for *G. harrisi*. We feel that the two species are probably synonymous. If so the name *cenomana* should presumably take priority, but we leave this matter pending further investigation.

RANGE. Appearing in the Middle Albian, this species is common in the Upper Albian, Cenomanian and Lower Turonian.

Subfamily **HETEROHELICINAE** Cushman 1927

Genus *HETEROHELIX* Ehrenberg 1843

TYPE SPECIES. *Spiroplecta americana* Ehrenberg 1844.

Heterohelix moremani (Cushman 1938)
(Plate 2, fig. 17)

1938 *Guembelina moremani* Cushman: 10, pl. 2, figs 1–3.
1940 *Guembelina washitensis* Tappan: 115; pl. 19, fig. 1.
1946 *Guembelina moremani* Cushman; Cushman: 103–104; pl. 46, figs 15, 16, not 17.
1962 *Heterohelix* sp. Ayala-Castanares: 11; pl. 1, fig. 1a–c; pl. 6, fig. 1a–c.
1967 *Heterohelix moremani* (Cushman) Pessagno: 260–261; pl. 48, figs 10–11; pl. 89, figs 1–2.

REMARKS. This species is very similar to *H. washitensis*, initially described from the Grayson Formation of Texas. The total range of *H. washitensis* was given by Tappan as Aptian to

Cenomanian. Tappan (1940) also noted the latter's similarity to *H. moremani*, but claimed that her species was smaller, possessed more horizontal sutures and had more globular chambers. The latter feature is not thought significant, as within a single population of *H. moremani* from the Upper Cenomanian all the extremes from nearly straight-sided to globose chambers are seen.

Pessagno (1967) noted that larger, gerontic specimens of *H. moremani*, such as the holotype, tend to show a more highly arched aperture, whereas the smaller specimens (which he figured on his pl. 48, figs 10–11) show low arched apertures. This, he claims, makes Tappan's differentiation, on the basis of the low aperture and smaller size, invalid. Therefore *H. washitensis* appears to be a junior synonym of *H. moremani.*

Bandy (1967) regards the two species as distinct and shows (fig. 11) that they follow each other in stratigraphic order. He also suggests they may be a dimorphic pair although, as he points out, this is unlikely as they have slightly different overall ranges. Bandy was prepared to accept *H. washitensis* as the ancestral form of *H. moremani*, and while this is the view held by ourselves, specific separation of the two forms is impossible.

RANGE. Middle Albian to Lower Turonian, although in the latter stage the number of individuals is greatly reduced.

Family **PLANOMALINIDAE** Bolli, Loeblich & Tappan 1957

Genus ***GLOBIGERINELLOIDES*** Cushman & ten Dam 1948

TYPE SPECIES. *Globigerinelloides algeriana* Cushman & ten Dam 1948.

Globigerinelloides bentonensis (Morrow 1934)

(Plate 1, fig. 11; Plate 2, figs 19, 20)

non 1927 *Anomalina eaglefordensis* Moreman: 99; pl. 16, fig. 9.
1934 *Anomalina bentonensis* Morrow: 201; pl. 30, fig. 4a–b.
1940 *Anomalina bentonensis* Morrow; Cushman: 28; pl. 5, fig. 3a–b.
non 1940 *Planulina eaglefordensis* (Moreman) Cushman: 32; pl. 6, figs 4, 5.
1946 *Anomalina bentonensis* Morrow; Cushman: 154; pl. 63, fig. 7a–b.
non 1946 *Planulina eaglefordensis* (Moreman); Cushman: 156; pl. 64, figs 8a–c, 9.
1957 *Planomalina caseyi* Bolli, Loeblich & Tappan: 24; pl. 1, figs 4a–5b.
1961b *Globigerinelloides bentonensis* (Morrow) Loeblich & Tappan: 267; pl. 2, figs 8–10.
non 1961b *Globigerinelloides eaglefordensis* (Moreman) Loeblich & Tappan: 268; pl. 2, figs 3a–7b.
non 1962 *Globigerinelloides eaglefordensis* (Moreman); Ayala-Castanares: 15–16; pl. 1, fig. 2a–c; pl. 6, figs 2a–b, 3a–b.
non 1964 *Globigerinelloides eaglefordensis* (Moreman); Loeblich & Tappan: C657–658, fig. 526, 7a–b.
1964 *Globigerinelloides caseyi* (Bolli, Loeblich & Tappan) Low: 122–123.
1965 *Globigerinelloides bentonensis* (Morrow); Eicher: 904; pl. 106, fig. 10.
1966 *Planomalina* (*Globigerinelloides*) *caseyi* (Bolli, Loeblich & Tappan); Salaj & Samuel: 161; pl. 6, fig. 1a–b.
1967 *Globigerinelloides bentonensis* (Morrow); Pessagno: 275; pl. 76, figs 10–11.
1967 *Globigerinelloides caseyi* (Bolli, Loeblich & Tappan); Pessagno: 276; pl. 49, figs 2–5.
1969a *Globigerinelloides caseyi* (Bolli, Loeblich & Tappan); Douglas: 161; pl. 5, fig. 9.
1970 *Globigerinelloides bentonensis* (Morrow); Eicher & Worstell: 297; pl. 8, figs 17a–b, 19a–b; pl. 9, figs 3a–b.
1970 *Globigerinelloides caseyi* (Bolli, Loeblich & Tappan); Eicher & Worstell: 297–298; pl. 8, figs 11, 15a–b, 16.
1972 *Globigerinelloides bentonensis* (Morrow); Gawor-Biedowa: 63–64; pl. 6, fig. 7a–c.

REMARKS. Initially described as an *Anomalina*, the planktonic nature of this species was not recognized for many years. Loeblich & Tappan (1961b), after inspecting the holotype, concluded that Morrow's species was better placed in the genus *Globigerinelloides.* In the same publication they placed *Anomalina eaglefordensis* in the same genus, recording that it differed from *G. bentonensis* in being smaller, less inflated and more evolute. *Planomalina caseyi*, originally described from the Gault Clay of England, was regarded as a junior synonym of *G. eaglefordensis.*

Pessagno (1967) confirmed Low's (1964) belief that *A. eaglefordensis* was a benthonic species and all the planktonic individuals referred to it ought to be placed in *G. caseyi*. However, many authors have noted the resemblance of *G. caseyi* (or *G. eaglefordensis*) to *G. bentonensis*. Low (1964) thought there were slight differences in the tightness of the coil and in the number of chambers in the final whorl, and kept the species separate, while Eicher (1965) considered them almost inseparable. In a more recent account Eicher & Worstell (1970) retain the two species while admitting the difficulties in so doing. The main differences recorded are the overall size, tightness of coiling, degree of inflation, and the rate of increase in size of the chambers. The present authors regard most of these variations as correlated with an increase in overall size. Eicher & Worstell's discussion of the distribution indicates that there is a possibility of ecological control. They report that specimens of *G. caseyi* occur in their upper planktonic zone while larger individuals of *G. bentonensis* are seen in the benthonic zone. Small specimens of both species occur in the benthonic zone and it is at this level that they found the greatest difficulty in distinguishing between them.

The initial concept of *G. caseyi* as a viable species is in doubt. Loeblich & Tappan (1961b) report that *G. eaglefordensis* (*G. caseyi*) has a diameter range of 0·15–0·31 mm, while *G. bentonensis* is generally larger (0·21–0·41 mm). This alone is no justification for the separation of the two species, but when all features are considered a case can be made out. In the Upper Gault Clay (Upper Albian) of England specimens of *G. caseyi* are usually small and would fall well within the range for the species indicated by Loeblich & Tappan. However, at certain levels within this clay sequence very large 'atypical' specimens are found. In all other ways these are identical with the smaller, more 'typical' members of the species. It would seem, therefore, that there is some form of environmental control on the overall size of the specimens.

Topotype specimens of *G. bentonensis* have been compared with topotype specimens of *G. caseyi* from Arlesey, England. Scanning electron photomicrographs of the two species appear almost identical and, even allowing for their stratigraphic separation, can only be regarded as synonymous. One feature shown by the specimens of *G. bentonensis* is the non-equatorial aperture. As all previous authors have described this species as possessing an equatorial aperture we assume that this variation is a feature peculiar to some of the specimens from the topotype locality and horizon.

Bandy (1967) recognizes *G. bentonensis* from the Cenomanian, as being derived from *G. escheri* Kaufman at the Albian/Cenomanian boundary. He also states that *G. caseyi* is a junior subjective synonym of *G. escheri*. Since *G. caseyi* and *G. bentonensis* are shown here to be synonymous, *G. escheri* is the valid name for the whole group. However, Bandy's figure (1967 : fig. 5) of *G. caseyi* is closer to that of *G. bentonensis* than it is to that of *G. escheri*, and it is more likely that *G. bentonensis* and *G. escheri* are distinct.

In England *G. bentonensis* appears in the Upper Albian with other planktonic species. At this level it is already completely differentiated from species of the genus *Hedbergella* Bronnimann & Brown, and Bandy's (1967) suggestion that it evolved from *G. blowi* (Bolli) in the Aptian is accepted.

RANGE. Upper Albian to Lower Cenomanian (in England), although rare specimens have been found throughout the whole Cenomanian sequence up to and including the Plenus Marls. Above this level specimens of *Globigerinelloides* would appear to be referable to *G. ehrenbergi* (Barr).

Family **SCHACKOINIDAE** Pokorný 1958

Genus ***SCHACKOINA*** Thalmann 1932

TYPE SPECIES. *Siderolina cenomana* Schacko 1897.

Schackoina cenomana (Schacko 1897)
(Plate 1, fig. 10)

1897 *Siderolina cenomana* Schacko: 166; pl. 4, figs 3–5.
1900 *Siderolina cenomana* Schacko; Egger: 174; pl. 21, fig. 42.
1928 *Siderolina cenomana* Schacko; Franke: 183; pl. 18, fig. 11a–c.
1930 *Hantkenina cenomana* (Schacko) Cushman & Wickenden: 40; pl. 6, figs 4–6.
1932 *Hantkenina* (*Schackoina*) *cenomana* (Schacko) Thalmann: 288.

1947 *Schackoina gandolfi* Reichel: 397, text-figs 3a–g, 6(3), 7(3), 8a, 10(1, 3, 4); pl. 8, fig. 1.
1951 *Schackoina cenomana* (Schacko); Noth: 74; pl. 5, figs 9–10.
1952 *Hastigerinoides rohri* Brönnimann: 55; text-fig. 29a–f; pl. 1, figs 8–9.
1954 *Schackoina gandolfi* Reichel; Aurouze & de Klasz: 99, text-fig. 1c.
1954 *Schackoina* sp. du groupe *cenomana* (Schacko); Aurouze & de Klasz: pl. 6a.
1955 *Schackoina cenomana* (Schacko); Montanaro-Gallitelli: 143–144.
1957 *Schackoina cenomana* (Schacko); Bolli, Loeblich & Tappan: 26; pl. 2, figs 1–2.
1959 *Schackoina gandolfi* Reichel; Bolli: 263; pl. 20, figs 12–18.
1959 *Schackoina cenomana* (Schacko); Bykova, Vasilenko, Voloshinova, Miatliuk & Subbotina: 300; text-fig. 676.
1959 *Schackoina cenomana* (Schacko); Orlov *et al.*: 300; text-fig. 676A–B.
1961b *Schackoina cenomana* (Schacko); Loeblich & Tappan: 270–271; pl. 1, figs 2–7.
1962 *Schackoina cenomana* (Schacko); Ayala-Castanares: 20–21; pl. 2, figs 2–3; pl. 7, fig. 3a–b; pl. 8, fig. 1a–c.
1964 *Schackoina cenomana* (Schacko); Loeblich & Tappan: C658, fig. 526, 8a–c, 9.
1966 *Schackoina cenomana* (Schacko); Salaj & Samuel: 165–166; pl. 7, fig. 8a–c.
1967 *Schackoina cenomana* (Schacko); Pessagno: 279; pl. 48, fig. 6.
1969 *Schackoina cenomana* (Schacko); Douglas: 162–163; pl. 6, fig. 5.
1969 *Schackoina cenomana* (Schacko); Scheibnerova: 57; pl. 7, figs 5–7.
1970 *Schackoina cenomana* (Schacko); Eicher & Worstell: 298; pl. 9, figs 1, 2, 4.
1972 *Schackoina cenomana cenomana* (Schacko); Gawor-Biedowa: 64–65; pl. 6, fig. 1.

Remarks. This species appears to be very rare in the British sequences, although this may reflect the processing techniques used during the present work. All the samples from south-west England had to be crushed under water – a method that may well destroy all trace of this very fragile species. However, in south-east England, where the Chalk is softer (and the necessary processing therefore less forceful), it is still extremely rare.

It appears to be the only representative of the genus in the British Isles, so very little can be said of its origin or development. In Britain it is first seen in the Middle Cenomanian; elsewhere the species has been recorded throughout the Cenomanian.

Range. Upper Cenomanian Zones 13 and 14(i) (iia) (=Plenus Marls Beds 1–3), and Lower Turonian, although rare specimens have been found in Cenomanian Zones 10–12.

Family **ROTALIPORIDAE** Sigal 1958

Subfamily **HEDBERGELLINAE** Loeblich & Tappan 1961

Genus ***HEDBERGELLA*** Brönnimann & Brown 1958

Type species. *Anomalina lorneiana* d'Orbigny var. *trochoidea* Gandolfi 1942.

Hedbergella amabilis Loeblich & Tappan 1961

(Plate 3, figs 22, 23)

1927 *Globigerina cretacea* d'Orbigny; Moreman: 100; pl. 16, fig 14–15.
1952 *Globigerina cretacea* d'Orbigny; Brönnimann: 14–16, text-fig. 3a–m.
1961b *Hedbergella amabilis* Loeblich & Tappan: 274; pl. 3, figs 1–10.
1961b *Clavihedbergella simplex* (Morrow); Loeblich & Tappan: 279–280; pl. 3, figs 11a–c, not figs 12–14.
1962 *Clavihedbergella simplex* (Morrow); Ayala-Castanares: 25–26; pl. 4, figs 2a–c, 3a–c, not fig. 1a–c; pl. 5, fig. 1a–c.
1963 *Hedbergella amabilis* Loeblich & Tappan; Renz, Luterbacher & Schneider: 1084; pl. 9, figs 4–6.
1964 *Clavihedbergella simplex* (Morrow); Todd & Low: 403–404; pl. 1, fig. 1.
1966 *Clavihedbergella amabilis* (Loeblich & Tappan) Salaj & Samuel: 173; pl. 10, fig. 3a–c.
1967 *Hedbergella amabilis* Loeblich & Tappan; Pessagno: 281–282; pl. 52, figs 6–8.
1969 *Hedbergella amabilis* Loeblich & Tappan; Douglas: 165; pl. 4, fig. 8.
1970 *Hedbergella amabilis* Loeblich & Tappan; Eicher & Worstell: 300, 302; pl. 9, figs 12, 13a–c.

Remarks. This species is very close in appearance to *Clavihedbergella simplex* (Morrow) and many authors have regarded the two as synonymous. However, recent accounts by Pessagno (1967) and Douglas (1969) indicate that they are distinct and have different ranges. Comparison of the type figures reveals that *H. amabilis* is larger than *C. simplex*, and lacks the radially elongated chambers

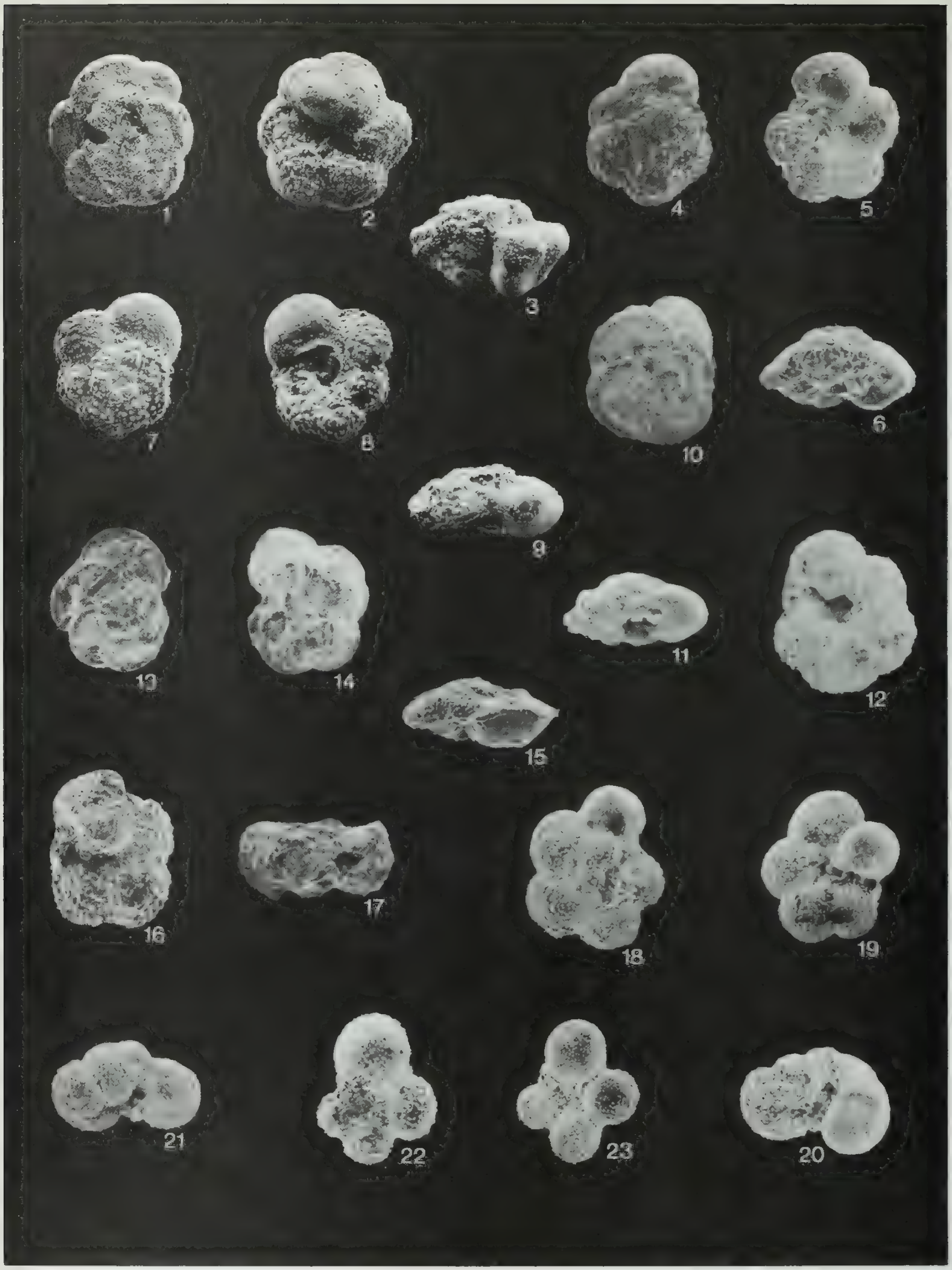
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Plate 3

Figs 1–3 *Praeglobotruncana algeriana* Caron. P 50006. Dorsal, ventral and peripheral views. Lowermost Turonian, Marnes à *Terebratella carentonensis*, Mezières s'Ballon, Sarthe, France. ×53.

characteristic of the latter, although the chambers of *H. amabilis* still must be described as subclavate. The topotype specimen of *H. amabilis* (Loeblich & Tappan 1961b : pl. 3, figs 1–10) shows a finely hispid test with a prominent apertural flap. The chambers are very slightly elongated, although this feature is over-emphasized by the very constricted sutures. *C. simplex* possesses a smooth surface with chambers that are very distinctly elongated. Loeblich & Tappan's paratypes of *H. amabilis* show great variation through a range which almost extends far enough to include *C. simplex*. Many authors think that the two species cannot be separated and regard the whole group as a single plexus. This may be the case, but because in England there occur representatives of *H. amabilis* only, this name is used here.

Many specimens of *H. amabilis* have almost rounded chambers and much less constricted sutures, thus showing a tendency to approach *H. delrioensis* (Carsey). *H. planispira* (Tappan) possesses the low spire characteristic of *H. amabilis*, but is much smaller.

In England *H. amabilis* appears sporadically throughout the Cenomanian and shows no close relationship with any other species. The true *C. simplex* has not been recorded. There is no link with the probably ancestral *H. planispira*, distinctions between the two species appearing suddenly at the Albian/Cenomanian boundary.

RANGE. Cenomanian Zones 7–14; also present in the Turonian in reduced numbers.

Hedbergella brittonensis Loeblich & Tappan 1961

(Plate 4, figs 13–15)

1934 *Globigerina cretacea* d'Orbigny; Morrow: 198; pl. 30, figs 7, 8, 10a–b.
1955 *Globigerina* cf. *G. cretacea* d'Orbigny; Applin: 196; pl. 48, figs 23–24.
1955 *Globigerina* sp. Küpper: 117; pl. 18, fig. 9a–c.
1961b *Hedbergella brittonensis* Loeblich & Tappan: 274–275; pl. 4, figs 1–8.
1961b *Hedbergella portsdownensis* (Williams-Mitchell) Loeblich & Tappan: 277; pl. 5, fig. 3a–c.
1967 *Globigerina portsdownensis* Williams-Mitchell; Bandy: 8, text-fig. 3.
1967 *Hedbergella brittonensis* Loeblich & Tappan; Fuchs: 331; pl. 18, fig. 1a–c.
1969b *Hedbergella portsdownensis* (Williams-Mitchell); Eicher: 168, fig. 3.
1969 *Hedbergella portsdownensis* (Williams-Mitchell); Douglas & Rankin: 194–196, fig. 7.
1970 *Hedbergella portsdownensis* (Williams-Mitchell); Eicher & Worstell: 304; pl. 10, figs 1a–c, 2a–b.
1972 *Hedbergella brittonensis* Loeblich & Tappan; Gawor-Biedowa: 67–68; pl. 8, figs 1a–c, 2a–c.

REMARKS. This species was erected by Loeblich & Tappan (1961) to include some of the forms placed in '*Globigerina cretacea*' but which possess an elevated spire. The dimensions of the holotype certainly demonstrate the elevation of the spire and the type figures display this feature

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Figs 4–6 *Praeglobotruncana hagni*/*P. algeriana* transitional form. P 50007. Dorsal, ventral and peripheral views. Lowermost Turonian Zone 14(iib), Bed C, Cenomanian Limestones, Bovey Lane Sandpit, Beer, near Seaton, Devon. × 50.

Figs 7–9 *Globotruncana* cf. *indica* (Pessagno *non* Jacob & Sastry). P 50010. Dorsal, ventral and peripheral views. Lowermost Turonian Zone 14(iib), Bed C, Cenomanian Limestones, Bovey Lane Sandpit, Beer, near Seaton, Devon. × 56.

Figs 10–12 *Praeglobotruncana hagni* Scheibnerova. P 50011. Dorsal, peripheral and ventral views. Lowermost Turonian, Marnes à *Terebratella carentonensis*, Mezières s'Ballon, Sarthe, France. Figs 4–5, × 51; Fig. 6, × 46.

Figs 13–15 *Rotalipora evoluta* Sigal. Fig. 13, P 50013, × 56; Figs 14–15, P 50014, × 45. Dorsal, ventral and peripheral views. Middle Cenomanian Zone 11(i), Beachy Head, near Eastbourne, Sussex.

Figs 16, 17 *Praeglobotruncana* cf. *helvetica* (Bolli). P 50015. Ventral and peripheral views. Lowermost Turonian Zone 14(iib), Bed C, Cenomanian Limestones, Bovey Lane Sandpit, Beer, near Seaton, Devon. × 45.

Figs 18–20 *Hedbergella infracretacea* (Glaessner). P 50016. Dorsal, ventral and peripheral views. Upper Albian Zone 6, Bed XIII, Cheriton, Folkestone, Kent. × 62.

Fig. 21 '*Hedbergella cretacea* (d'Orbigny).' P 50017. Peripheral view. Upper Cenomanian Zone 14(iia), Bed C, Cenomanian Limestones, Bovey Lane Sandpit, Beer, near Seaton, Devon. × 54.

Figs 22, 23 *Hedbergella amabilis* Loeblich & Tappan. P 50018–9. Dorsal and ventral views. Upper Cenomanian Zone 13, Maiden Newton, Dorset. Fig. 22, × 69; Fig. 23, × 96.

clearly. However, in the same publication Loeblich & Tappan refer closely similar individuals to the species *H. portsdownensis*. Although they claim that this species has a low spire, they illustrate (1961 : pl. 5, fig. 3a–c) a specimen with a spire equal to, if not higher than, that in some of the figures of *H. brittonensis*.

This would appear to invalidate *H. brittonensis* on grounds of priority, but an added complication has arisen. Loeblich & Tappan (1961) do not mention the type specimen of *H. portsdownensis* and only figure hypotypes from the Cenomanian of Germany. Eicher & Worstell (1970) were misled by this inclusion of German specimens into assuming that the species had been described originally from the Cenomanian of Germany.

The holotype (P 38283) of *H. portsdownensis* in the British Museum (Natural History), London, has been inspected and the original description of the species found incorrect. Williams-Mitchell's (1948) description refers to specimens commonly seen in the Upper Cenomanian of England, in which the final chamber typically overhangs the umbilicus. Unfortuntaely the holotype does not show this feature and would be better placed in *H. delrioensis*. The spire certainly is not elevated enough to warrant specific separation and it is not at all like that illustrated by Loeblich & Tappan (1961) as typical of the species. If *H. portsdownensis* is a junior synonym of *H. delrioensis*, then *H. brittonensis* in our sense becomes the valid name for those high-spired Cenomanian forms ascribed to *H. delrioensis*. However, there is, in any population, a full range from the lower-spired, typical *H. delrioensis* to the high-spired, typical *H. brittonensis*, and not even a mathematical approach permits their satisfactory separation. The two names are used here to refer to the end members of the plexus. However, recent communications with workers in the U.S.A. show that the type specimens of *H. brittonensis* may not be as high-spired as the type descriptions and figures suggest. If this proves correct there will be no satisfactory name for the species. Nevertheless, until the holotypes can be examined the name *H. brittonensis* is retained.

Williams-Mitchell (1948) confined *H. portsdownensis* to the Cenomanian, and while we do not condone the practice of changing specific names at stratigraphic boundaries, *H. infracretacea* (Glaessner 1966) is used for the earlier Albian forms of the same plexus. The latter, although similar in external characteristics, is generally much smaller and usually displays a more overhanging final chamber.

RANGE. Mainly Cenomanian Zones 7–14(iia) (Plenus Marls Bed 3); some individuals have been encountered in the Lower Turonian.

'***Hedbergella cretacea*** (d'Orbigny 1840)'
(Plate 3, fig. 21)

A full synonymy has not been prepared as the individuals discussed here are not typical of d'Orbigny's species.

REMARKS. D'Orbigny's species has been cited by many authors for any planktonic foraminifer seen in rocks younger than the Lower Cretaceous. Brady (1884) even listed it as a Recent species. However, during the last decade there have been several attempts to rationalize our understanding of *Globigerina cretacea* d'Orbigny. Some of these have clarified, while others have confused the situation. While we do not intend to repeat these arguments, additional data relating to the origin of this species is presented.

Globigerina cretacea d'Orbigny was originally described in 1840 from the White Chalk of St Germain, near Paris. This bed is regarded as Lower Campanian in age. In 1960 Banner & Blow redescribed d'Orbigny's original specimens. They found only one phial of specimens from St Germain in the Musée d'Histoire Naturelle in Paris and selected the most complete specimen from the syntypic series as the lectotype (Banner & Blow 1960 : 8: pl. 7, fig. 1). The diagnosis they gave was very like that of d'Orbigny but differed in two respects. The lectotype was seen to possess two broadly spaced yet weakly developed keels, and it was assumed that these had not been seen by d'Orbigny. Other specimens in d'Orbigny's collection, appearing conspecific with the lectotype, possess well-preserved tegillae. These facts, in Banner & Blow's opinion, placed the species in the genus *Globotruncana* Cushman, which ranges from Coniacian? to Campanian.

Hofker (1961), unaware of Banner & Blow's work, cites Marie (1941) as recording only two planktonic foraminifera in the 'Craie Blanche' at Meudon (*Globigerina aspera* Ehrenberg and *Globigerina cretacea* d'Orbigny). Hofker's summary of the main morphological features of *G. cretacea* did not include the presence of widely spaced, twin keels. Hofker did not attempt to produce a full synonymy and gave only important references to the species. This summary indicated that the range of the species, as quoted by the various authors, was totally indecisive.

Hagn (1953 : 92; pl. 8, fig. 5) recorded *G. cretacea* from the lower Upper Campanian and indicated that it was found also in the Albian and Cenomanian where it was best referred to *G. infracretacea* Glaessner. Hofker (1961) summarized the development of *G. cretacea* from Glaessner's species as follows:

Aptian – Albian	*Praeglobotruncana infracretacea* (Glaessner) form
Albian – Cenomanian . . .	*Praeglobotruncana* sp., cf. *P. gautierensis* (Brönnimann) form
Cenomanian – Turonian . . .	*Praeglobotruncana crassa* Bolli form
Turonian – Upper Campanian . .	*Globigerina cretacea* d'Orbigny form, with weak ornament
Lower – Upper Maastrichtian . .	*Globigerina cretacea* d'Orbigny form, with strong ornament
Upper Maastrichtian	*Rugoglobigerina rugosa* (Plummer) form – culminating in aberrant forms.

Bandy (1967), without referring to Hofker, and using very different generic determinations, produced a basically similar scheme. However, on the basis of the thinner wall structure, rugose surface, character of the umbilical plate, slope of the chambers and the geological range, he favoured an affinity with the genus *Rugoglobigerina* Bronnimann rather than *Globotruncana* Cushman. Bandy rejects an origin for *G. cretacea* from the *Rugoglobigerina* stock, the *Globotruncana linneiana bulloides* Vogler lineage or the *Praeglobotruncana delrioensis* (Plummer) lineage. He considers it derived from *Hedbergella trochoidea* (Gandolfi), which, at higher levels, does show a tendency to expand its porticus, a process which, if continued, could lead to the formation of a tegilla. Bandy also interpreted the development of faint keels as parallel evolution with *Globotruncana*. Bandy's views differ from those of Hofker only in including the twin keels in the final determination of the species. Both workers consider *R. rugosa* (Plummer) an end member of the lineage.

Pessagno (1967) erected the new genus *Archaeoglobigerina* Pessagno, and a new species (*A. blowi* Pessagno 1967) for specimens immediately ancestral to *A. cretacea* (d'Orbigny). Pessagno records the presence of transitional forms between these two species and an '*A. blowi* stage' in the early whorls of some specimens of '*A. cretacea*'. *A. blowi* is recorded from the Coniacian and Santonian while *A. cretacea* is restricted to the Santonian and Lower Maastrichtian interval. Pessagno was dissatisfied with Banner & Blow's selection of a lectotype, on the grounds that d'Orbigny appeared to indicate a specimen with a more lobulate periphery and a more rapid increase in chamber size in the last whorl. Douglas (1969), however, places *A. cretacea* within the genus *Globotruncana*.

Work on the Albian–Lower Turonian interval shows that the *G. cretacea* lineage originated from *Hedbergella*. Many individuals have been found in the Upper Cenomanian which possess a faint trace of twin keels on some of the chambers of the final whorl. These, but for these faint keels, would be referred to *H. delrioensis* (Carsey), and it is suggested that this species is the initial source of the *G. cretacea* group. In the Albian–Cenomanian interval there is, as already noted, a plexus including *H. infracretacea* (Glaessner), *H. delrioensis* (Carsey) and *H. brittonensis* Loeblich & Tappan. This evolutionary lineage is included in Fig. 7.

Although the generic determination in the upper levels of the Cretaceous is still in dispute the forms from the Cenomanian, in all but one character, belong in the genus *Hedbergella*. In the Cenomanian apertural modifications are not apparent. The apertural characteristics place these individuals within *Hedbergella*. The 'keels' are not typical of those seen in the *Globotruncana* group, but are produced by an alignment of the surface ornament. This is all these structures ever become, even in the Maastrichtian, although some of Pessagno's figures indicate structures more prominent than those normally encountered. As these keels are not of the same structure as the normal globotruncanid keel it is thought best to retain the Cenomanian individuals within the genus *Hedbergella*.

RANGE. Rarely seen in the Upper Cenomanian Zone 13, more abundant in the Lower Turonian.

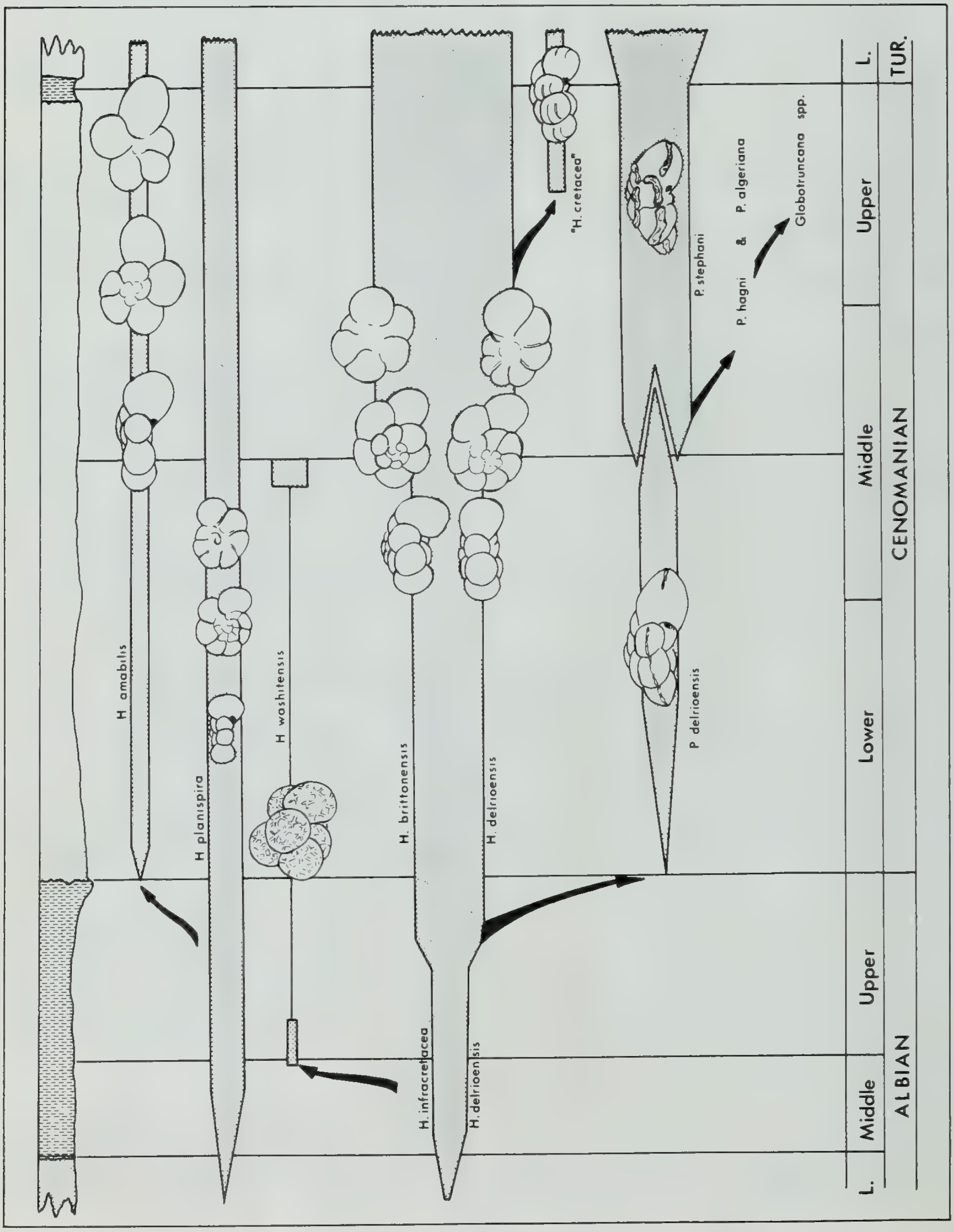
H amabilis
H planispira
H washitensis
H. brittonensis
H. delrioensis
H. infracretacea
H. delrioensis
"H. cretacea"
P delrioensis
P. stephani
P. hagni & P. algeriana
Globotruncana spp.
L.
Middle
Upper
Lower
Middle
Upper
L.
ALBIAN
CENOMANIAN
TUR.

Fig. 7 Evolution of the *Hedbergella* and *Praeglobotruncana* groups.

Hedbergella delrioensis (Carsey 1926)
(Plate 4, figs 1–3)

1926 *Globigerina cretacea* d'Orbigny var. *delrioensis* Carsey: 43.
? 1940 *Globigerina cretacea* d'Orbigny; Tappan: 121–122; pl. 19, fig. 11.
? 1943 *Globigerina cretacea* d'Orbigny; Tappan: 512; pl. 82, figs 16–17.
1952 *Globigerina gautierensis* Bronnimann: 11; pl. 1, figs 1–3; text-fig. 2a–c.
1954 *Globigerina delrioensis* Carsey; Frizzell: 127; pl. 20, fig. 1.
1959 *Praeglobotruncana gautierensis* (Brönnimann) Bolli: 265; pl. 21, figs 3–6.
1959 *Praeglobotruncana* (*Hedbergella*) *delrioensis* (Carsey) Banner & Blow: 8.
1960 *Praeglobotruncana gautierensis* (Brönnimann); Jones: 102; pl. 15, figs 1a–c, 2a–c, ? 3, ? 4, 5, ? 6, 7a–c, 8, 9a–c; text-fig. 1.
1962 *Praeglobotruncana gautierensis* (Brönnimann); Pessagno: 358; pl. 6, fig. 4.
1962 *Hedbergella delrioensis* (Carsey) Takayanagi & Iwamoto: 190; pl. 28, figs 10–12.
1963 *Hedbergella delrioensis* (Carsey); Renz, Luterbacher & Schneider: 1083; pl. 9, fig. 5a–c.
1964 *Hedbergella delrioensis* (Carsey); Todd & Low: 402; pl. 1, fig. 2a–c.
1966 *Hedbergella delrioensis* (Carsey); Salaj & Samuel: 167; pl. 8, fig. 5a–c.
1966 *Hedbergella delrioensis* (Carsey); Butt: 173–174; pl. 2, figs 1–8.
1966 *Hedbergella delrioensis* (Carsey); Eicher: 27; pl. 5, fig. 12.
1967 *Hedbergella delrioensis* (Carsey); Pessagno: 282–283; pl. 48, figs 1, 2, 3–5.
1967 *Hedbergella delrioensis* (Carsey); Eicher: 186; pl. 19, fig. 6.
1969b *Hedbergella delrioensis* (Carsey); Eicher: 168, fig. 3.
1970 *Hedbergella delrioensis* (Carsey); Eicher & Worstell: 302; pl. 9, figs 10, 11a–b.

REMARKS. The authors follow the majority of previous workers in their determinations and include within this species all those individuals occurring in the Albian to Turonian interval which possess a moderate to low spire. There is a complete range within *Hedbergella* from forms with an almost flat (*H. planispira* (Tappan)) to a very high spire (*H. brittonensis* Loeblich & Tappan). Many authors have proposed separate specific names for extreme forms and many of the intermediates in the series. However, the authors believe that the variation is continuous and not naturally subdivisible. In the present work, for convenience, the end members of the plexus have been retained as separate species.

The most abundant planktonic species found in the Neocomian to Aptian interval is *Globigerina kugleri* Bolli. This is thought to have evolved into *H. delrioensis* by the development of an extraumbilical aperture and the addition of another chamber in the final whorl. Bandy (1967) considered *H. delrioensis* as the basic stock from which evolved *Globigerinelloides* Cushman & ten Dam, *Hedbergella* Bronnimann & Brown, *Praeglobotruncana* Bermudez, *Schackoina* Thalmann, *Clavihedbergella* Banner & Blow, *Ticinella* Reichel, *Rotalipora* Brotzen and *Globotruncana* Cushman. Bandy's hypothesis is supported by the present research.

RANGE. Recorded from the Middle Albian Zone 4 to the Lower Turonian – although Takayanagi (1965) gives the complete range as Neocomian–Santonian.

Hedbergella infracretacea (Glaessner 1937)
(Plate 3, figs 18–20)

1890 *Globigerina cretacea* d'Orbigny; Burrows, Sherborn & Bailey: 561; pl. 11, fig. 18.
1892 *Globigerina cretacea* d'Orbigny; Chapman: 517; pl. 15, fig. 13.
1896 *Globigerina bulloides* d'Orbigny; Chapman: 587; pl. 13, fig. 4a–b.
1896 *Globigerina cretacea* d'Orbigny; Chapman: 588; pl. 13, figs 5–6.
1935a *Globigerina cretacea* d'Orbigny; Eichenberg: 30–31; pl. 6, fig. 4.
1935b *Globigerina cretacea* d'Orbigny; Eichenberg: 395; pl. 5, figs 53–54.
1937 *Globigerina infracretacea* Glaessner: 28; text-fig. 1.
? 1940 *Globigerina cretacea* d'Orbigny; Tappan: 121–122; pl. 19, fig. 11a–c.
? 1943 *Globigerina cretacea* d'Orbigny; Tappan: 512; pl. 82, figs 16–17.
1947 *Globigerina infracretacea* Glaessner; ten Dam: 27–28.
1948a *Globigerina infracretacea* Glaessner; ten Dam: 188–189.
1950 *Globigerina infracretacea* Glaessner; ten Dam: 54.
1951 *Globigerina infracretacea* Glaessner; Noth: 73; pl. 7, fig. 51.
1953 *Globigerina infracretacea* Glaessner; Subbotina: 51; pl. 1, figs 5–10.

1954 *Globigerina infracretacea* Glaessner; Bartenstein: 49.
1957 *Globigerina infracretacea* Glaessner; Said & Bakarat: 45; pl. 1, fig. 27a–c.
1959 *Praeglobotruncana infracretacea* (Glaessner) Bolli: 266; pl. 21, figs 9, 10; not pl. 22, fig. 1.
1960 *Globigerina infracretacea* Glaessner; Tollmann: 191; pl. 20, figs 4–5.
1960a *Globigerina infracretacea* Glaessner; Moullade: 136; pl. 2, figs 18–20.
1961 *Praeglobotruncana infracretacea* (Glaessner); Hofker: 96.
1961b *Globigerina infracretacea* Glaessner; Loeblich & Tappan: 276.
1963 *Hedbergella delrioensis* (Carsey); Maslakova: 114 (part).
1963 *Hedbergella infracretacea* (Glaessner) Renz, Luterbacher & Schneider: 1083.
1965 *Globigerina infracretacea* Glaessner; Neagu: 36; pl. 10, figs 10–12.
1966 *Hedbergella infracretacea* (Glaessner); Salaj & Samuel: 169; pl. 8, fig. 8a–c.
1966 *Hedbergella infracretacea* (Glaessner); Glaessner (emend.): 179–183; pl. 1, figs 1–3.
1967 *Hedbergella infracretacea* (Glaessner); Fuchs: 331; pl. 17, fig. 13a–c.
1967 *Hedbergella infracretacea* (Glaessner); Uguzzoni & Radrizzani: 1226; pl. 92, figs 7a–c, 8a–b.
1972 *Hedbergella infracretacea* (Glaessner); Gawor-Biedowa: 69–70; pl. 6, fig. 8a–c.

REMARKS. This species has been emended by Glaessner, who noted the great variation both in elevation of the spire and position of the aperture. In 1961 Loeblich & Tappan regarded *H. infracretacea* as similar to, and possibly synonymous with, *H. delrioensis*, differing only in being half the size. Glaessner, after studying the type specimens, concluded that *H. infracretacea* could be differentiated by its higher spire and relatively smaller size. *H. infracretacea* is now regarded as a morphologically primitive member of the genus *Hedbergella*.

RANGE. Middle and Upper Albian Zones 4–6.

Hedbergella planispira (Tappan 1940)
(Plate 4, figs 4–6)

1940 *Globigerina planispira* Tappan: 12; pl. 19, fig. 12.
1943 *Globigerina planispira* Tappan; Tappan: 513; pl. 83, fig. 3.
1948 *Globigerina almadenensis* Cushman & Todd: 95; pl. 16, figs 18, 19.
1949 *Globigerina globigerinelloides* Subbotina: 32; pl. 2, figs 11–16.
1953 *Globigerina globigerinelloides* Subbotina; Subbotina: pl. 1, figs 11, 12.
1954 *Globorotalia ? youngi* Fox: 119; pl. 26, figs 15–18.
1956 *Hedbergina seminolensis* (Harlton); Brönnimann & Brown: 529; pl. 20, figs 4–6.
1957a *Praeglobotruncana planispira* (Tappan) Bolli, Loeblich & Tappan: 40; pl. 9, fig. 3.
1959 *Praeglobotruncana modesta* Bolli: 267; pl. 22, fig. 2.
1959 *Praeglobotruncana planispira* (Tappan); Bolli: 267; pl. 22, figs 3–4.
1961b *Hedbergella planispira* (Tappan) Loeblich & Tappan: 276–277; pl. 5, figs 4–11.
1964 *Hedbergella planispira* (Tappan); Olsson: 161–162; pl. 1, figs 4, 5.
1964 *Hedbergella planispira* (Tappan); Todd & Low: 402.
1965 *Hedbergella planispira* (Tappan); Takayanagi: 205; pl. 21, figs 6a–7c.
1965 *Hedbergella planispira* (Tappan); Eicher: 905; pl. 106, fig. 1.
1967 *Hedbergella planispira* (Tappan); Pessagno: 283–284; pl. 51, fig. 1; pl. 53, figs 1–4.
1967 *Hedbergella planispira* (Tappan); Eicher: 186; pl. 19, fig. 3.
1969b *Hedbergella planispira* (Tappan); Eicher: 168, text-fig. 3.
1969b *Hedbergella planispira* (Tappan); Douglas: 168; pl. 5, fig. 1.
1970 *Hedbergella planispira* (Tappan); Eicher & Worstell: 302, 304; pl. 9, figs 12, 13a–c.
1972 *Hedbergella planispira* (Tappan); Gawor-Biedowa: 70–71; pl. 5, fig. 8a–c.

REMARKS. This small, distinctive species is found throughout the greater part of the Albian and Cenomanian in England. Although the majority of the specimens are characteristic of the species as generally understood, occasionally larger, more robust specimens are encountered. These may belong to *H. trochoidea* (Gandolfi).

The dimensions of *H. planispira* and *H. trochoidea* given by Loeblich & Tappan (1961b) are as follows.

H. planispira – holotype diameter 0·24 mm; thickness 0·11 mm
range of diameter 0·11–0·26 mm
H. trochoidea – holotype diameter 0·39 mm; thickness 0·18 mm
range of diameter 0·26–0·39 mm

Loeblich & Tappan suggested that *H. trochoidea* differs from *H. planispira* in being three times as large, displaying greater increase in chamber size and a more rugose surface, but the figures quoted above show that there is no firm dividing line between the two species. In many of the species of *Hedbergella* larger chambers usually display a coarser rugosity and neither chamber size nor rugosity can be relied on for specific differentiation. In England forms very similar to *H. trochoidea* occur at certain levels and there is a possibility that these are ecophenotypic variants of *H. planispira*. This relationship would explain the difficulty many workers have found in differentiating these species. Other specimens could equally well be placed in *H. delrioensis*, and many workers prefer to regard this as a synonym. In the present work no specimens have been found that can be certainly referred to *H. trochoidea*.

RANGE. Middle Albian Zone 4 to Upper Cenomanian Zone 14; occurs in reduced numbers in the Lower Turonian.

Hedbergella washitensis (Carsey 1926)
(Plate 2, fig. 16)

1926 *Globigerina washitensis* Carsey: 44; pl. 7, fig. 10; pl. 8, fig. 2.
1931 *Globigerina washitensis* Carsey; Plummer: 193; pl. 13, fig. 12.
1940 *Globigerina washitensis* Carsey; Tappan: 122; pl. 19, fig. 13.
1943 *Globigerina washitensis* Carsey; Tappan: 513; pl. 83, figs 1–2.
1944 *Globigerina washitensis* Carsey; Lozo: 563; pl. 3, fig. 4.
1949 *Globigerina washitensis* Carsey; Loeblich & Tappan: 265; pl. 51, fig. 4.
1954 *Globigerina washitensis* Carsey; Frizzell: 127; pl. 20, fig. 9.
1956 *Globigerina washitensis* Carsey; Bolin: 293; pl. 39, figs 2–3; text-fig. 5 (11a–b).
1959 *Globigerina washitensis* Carsey; Bolli: 271; pl. 23, figs 6–7.
1961b *Hedbergella washitensis* (Carsey) Loeblich & Tappan: 278; pl. 4, figs 9–11.
1962 *Hedbergella washitensis* (Carsey); Ayala-Castanares: 22; pl. 2, fig 1a–c.
1967 *Hedbergella washitensis* (Carsey); Pessagno: 284–285; pl. 49, fig. 1.
1967 *Globigerina washitensis* Carsey; Bandy: 8; text-fig. 3.

REMARKS. The very characteristic appearance of this species is reflected in the unanimity of the synonymy. The only apparent dissension is that of Bandy (1967), who returns this species to the genus *Globigerina*. We feel that this is not justified, as the development of the species from the *H. infracretacea* (Glaessner) stock is probable. The latter often shows the final chamber overhanging the umbilicus, and little modification would be required to produce the highly enrolled *H. washitensis*.

The distribution of this species in England is interesting and requires discussion. Although rare specimens have been found in the upper part of the Gault Clay (Upper Albian) and in the lowermost Lower Chalk (Lower Cenomanian) there are only two levels where specimens can be regularly found. The first is at the non-sequence at the base of the Upper Gault Clay (*cristatum* Subzone). The forms seen at this level approach *H. hiltermanni* Loeblich & Tappan, possess a coarser ornament and are generally flatter-spired than those found at the other level of abundance, which occurs immediately prior to the major non-sequence in the mid-Cenomanian (Carter & Hart in the discussion of Kennedy 1969). In the Chalk *H. washitensis* can be used as an indicator of the latter level throughout the whole of southern England.

The more important occurrences of this species are in close stratigraphic proximity to non-sequences and erosion surfaces, and therefore indicate that this species may only be an ecologically controlled variant of *Hedbergella* produced by the changing environments that preceded such features. A change of environment is suggested by the macrofauna, especially in the mid-Cenomanian, where *H. washitensis* is restricted to a band containing abundant *Orbirhynchia mantelliana* (J. Sowerby). In his account of the Lower Chalk Kennedy (1969) does not give reasons for concentration of brachiopods in this band. The occurrence of *H. washitensis* in the Cenomanian Sands of Devon is significant, as these were deposited in a shallow sea very close to the Cenomanian shoreline. Recent research has produced specimens of *H. delrioensis* from even nearer the shoreline (from the Haldon Hills – see Fig. 1, p. 5). In these marginal areas the surface reticulation is slightly different from that on specimens from the south-east of England, and this change could be ecologically induced.

RANGE. Appearing at the base of the Upper Albian the species is found up to the *O. mantelliana* Band, immediately preceding the mid-Cenomanian non-sequence.

Genus ***PRAEGLOBOTRUNCANA*** Bermudez 1952

TYPE SPECIES. *Globorotalia delrioensis* Plummer 1931.

Praeglobotruncana algeriana Caron 1966
(Plate 3, figs 1–3)

1936 *Globotruncana appenninica – Globotruncana linnei* Renz: 34; pl. 6, figs 18–20; table 8, fig. 2.
1945 *Globotruncana renzi* Thalmann: 405.
1949 *Globotruncana* (*Globotruncana*) aff. *renzi* Thalmann-Gandolfi; Reichel: 612–613; pl. 16, fig. 8, pl. 17, fig. 8.
1960a *Praeglobotruncana renzi* (Thalmann) Klaus: 795–796; pl. 6, fig. 4a–c.
1961a *Praeglobotruncana renzi* (Thalmann); Malapris & Rat: 90–91; pl. 2, fig. 5a–c; text-fig. 6.
1966 *Praeglobotruncana renzi* (Thalmann); Eicher: 28–29; pl. 6, fig. 9.
1966 *Praeglobotruncana algeriana* Caron: 74–75.
1966 *Praeglobotruncana* cf. *algeriana* Caron; Caron: 75–76; pl. 2, fig. 5a–c.
1969 *Praeglobotruncana algeriana* Caron; Neagu: 142; pl. 17, figs 8–15; pl. 20, figs 4–6; pl. 22, figs 7–8; pl. 23, figs 1–2.

REMARKS. This species is very close to *P. hagni* Scheibnerova, and several specimens from the Plenus Marls appear intermediate between the two forms (see Pl. 3, figs 4–6). Both arise from the *P. delrioensis* (Plummer)/*P. stephani* (Gandolfi) lineage in the Upper Cenomanian, although they only attain their maximum development in the Lower Turonian. The main difference between this species and *P. hagni* is in the more elevated dorsal side and the slightly less convex ventral side. Butt (1966), in his figures of *P. hagni*, included several individuals very similar to *P. algeriana*, and a study of the holotypes may prove the two to be synonymous.

Neagu (1969) recorded this species as the earliest member of the twin-keeled *Praeglobotruncana* group found in the eastern Carpathians, but in Britain *P. hagni* has been recorded at a lower level, although specimens are rare.

RANGE. Upper Cenomanian Zone 13, Plenus Marls Zone 14; continuing into the Lower Turonian in greater numbers.

Praeglobotruncana delrioensis (Plummer 1931)
(Plate 4, figs 22–24)

1931 *Globorotalia delrioensis* Plummer: 199; pl. 13, fig. 2a–c.
non 1940 *Globorotalia delrioensis* Plummer; Tappan: 123; pl. 19, fig. 14.
1946 *Globorotalia marginaculeata* Loeblich & Tappan: 257; pl. 37, figs 19–21; text-fig. 4a.
non 1946 *Globorotalia delrioensis* Plummer; Loeblich & Tappan: 257; text-fig. 4b.
1950 *Globotruncana stephani* Gandolfi; Mornod: 587; pl. 15, figs 9a–r, 10, 17; text-fig. 10(1–3).
1952 *Praeglobotruncana delrioensis* (Plummer) Bermudez: 52; pl. 7, fig. 1.
1954 *Globorotalia delrioensis* Plummer; Frizzell: 129; pl. 20, fig. 27.
1954 *Globotruncana stephani* Gandolfi; Hagn & Zeil: 33; pl. 2, fig. 7; pl. 5, figs 7–8.
1956 *Praeglobotruncana delrioensis* (Plummer); Brönnimann & Brown: 53; pl. 21, figs 8–10; pl. 24, figs ? 16, 17, text-figs 9, 13a, b, d, ? 15c–f; not text-figs 16c, d, e.
1957 *Praeglobotruncana delrioensis* (Plummer); Bolli, Loeblich & Tappan: 39; pl. 9, fig. 1.
1957 *Praeglobotruncana* cf. *delrioensis* (Plummer); Bolli, Loeblich & Tappan: 55; pl. 12, fig. 4.
non 1957 *Praeglobotruncana delrioensis* (Plummer); Zeigler: 199.
1959 *Praeglobotruncana* (*Praeglobotruncana*) sp. cf. *stephani* (Gandolfi); Banner & Blow: pl. 3, fig. 4.
1960a *Praeglobotruncana delrioensis* (Plummer); Klaus: 793–794; pl. 6, fig. 1a–c.
1960b *Praeglobotruncana delrioensis* (Plummer); Klaus: 300–301, text-fig. 1a.
1961b *Praeglobotruncana delrioensis* (Plummer); Loeblich & Tappan: 280–284; pl. 6, figs 9–12.
1963 *Praeglobotruncana delrioensis* (Plummer); Salaj & Samuel: 104–105; tab. 6, fig. 4a–c.

non 1964 *Praeglobotruncana delrioensis* (Plummer); Todd & Low: 404; pl. 2, fig. 4.
1966 *Praeglobotruncana delrioensis* (Plummer); Salaj & Samuel: 188; pl. 15, fig. 3a–c.
1967 *Praeglobotruncana delrioensis* (Plummer); Pessagno: 286–287; pl. 52, figs 3–5; pl. 100, fig. 7.

REMARKS. This species has been confused in the literature with *P. stephani* (Gandolfi) and was regarded as synonymous with it by Bronnimann & Brown (1956 : 531), Zeigler (1957 : 199) and Banner & Blow (1959 : 8).

Loeblich & Tappan (1961b) claim that the two species are quite distinct. They also claim that there is great variation within *P. delrioensis* and include *P. marginaculeata* (Loeblich & Tappan) within its synonymy. However, when studying complete sequences of strata sampled at close, regular intervals, none of these species can be separated. It is true that the type specimens are distinct – hence the retention of the specific names – but it is also clear that they belong in a single evolutionary plexus beginning with *P. delrioensis.* This has already been recognized by Klaus (1960b : 285–308), who showed, using statistical methods, that all three species belong to the one lineage. The overlap of characters makes accurate differentiation impossible, and *P. delrioensis* is seen to evolve imperceptibly into *P. stephani* during the mid-Cenomanian.

P. delrioensis probably evolved from *Hedbergella delrioensis* in the lowermost Cenomanian, and the first transitional forms appear at the Albian/Cenomanian boundary irrespective of the facies involved.

RANGE. Lower Cenomanian Zones 7–11(i).

Praeglobotruncana hagni Scheibnerova 1962
(Plate 3, figs 10–12)

1962 *Praeglobotruncana hagni* Scheibnerova: 219, 225–226; text-fig. 6a–c.
1966 *Praeglobotruncana hagni* Scheibnerova; Caron: 76; pl. 2, fig. 6a–c.
1966 *Praeglobotruncana* sp. cf. *P. hagni* Scheibnerova; Butt: 174; pl. 3, figs 1, ? 2, ? 3, ? 4.

REMARKS. *P. hagni* is normally characterized by an almost flat dorsal surface, although some specimens with a convex dorsal surface have been found. All specimens have a more or less developed double keel. The aperture is largely extraumbilical and this places the species within the definition of *Praeglobotruncana.*

The species is probably synonymous with *Globotruncana roddai* (Marianos & Zingula 1966 : 340; pl. 39, fig. 6a–c). Douglas (1969a, b) also described this species from the Turonian of California, including it in *Praeglobotruncana.* His illustrations of *P. roddai*, as well as its recorded position in the California succession, shows it to be a junior synonym of *P. hagni.*

P. hagni, while appearing in the Upper Cenomanian, is more frequently found in the Lower Turonian, especially in the lower levels of the Frétevou Chalk (Butt 1966). Similar numbers are found only in the upper beds of the Plenus Marls, and the lower levels of the Middle Chalk. The relationship of the British and French populations will be discussed in the following stratigraphic account.

RANGE. Upper Cenomanian Zones 13–14; Lower Turonian, with levels of greater abundance in Zone 14(iib) (Plenus Marls Beds 4–8).

Praeglobotruncana cf. ***helvetica*** (Bolli 1945)
(Plate 3, figs 16–17)

cf. 1945 *Globotruncana helvetica* Bolli: 226; pl. 9, figs 6–8; text-fig. 1 (9–12).

REMARKS. This typically Turonian species has not been studied in detail as few specimens have been found. In the upper levels of the Plenus Marls (Beds 4–8) atypical forms have been found – adding weight to the placing of the Cenomanian/Turonian boundary at a level within the marl unit.

The main feature of interest are the rare finds of specimens of a '*helvetica*' type in Zone 13 of the Upper Cenomanian. Some of the specimens are very close to *P. helvetica*, while others appear to be closely similar to *Hedbergella delrioensis*, having developed a very flat spire and the faint trace of the characteristic *Praeglobotruncana* keel. This indicates that *P. helvetica* may have developed from the *H. delrioensis* lineage instead of from the *P. delrioensis* lineage as was suggested by Bandy (1967). He postulated that by development of a flat dorsal surface and inflation of the chambers ventrally *P. helvetica* could have been produced from *P. delrioensis*. However, the *Praeglobotruncana* lineage does not show this transition to a lower spire. The main trend through *P. stephani* to forms described as *P. stephani* var. *turbinata* Reichel indicates a progressive increase in spire height. The only reduction of this feature is seen in the transitional sequence through *P. hagni* to *Globotruncana* cf. *indica* Jacob & Sastri of Pessagno, which is accompanied by the development of the second keel, there being no indication of any trend towards a form that could be related to *P. helvetica*.

RANGE. Very primitive forms have been found in the Upper Cenomanian, although typical specimens are only encountered in the overlying Turonian.

Praeglobotruncana stephani (Gandolfi 1942)

(Plate 4, figs 16–21)

1942 *Globotruncana stephani* Gandolfi: 130; pl. 3, figs 4, 5; pl. 4, figs 36, 37, 41–45; pl. 6, figs 4, 6; pl. 9, figs 5, 8; pl. 13, fig. 5; pl. 14, fig. 2.
1942 *Globotruncana appenninica* var. *beta* Gandolfi: 119, text-fig. 41 (2a–b).
1945 *Globotruncana stephani* Gandolfi; Bolli: 224 (part); text-fig. 1 (3, 4); pl. 9, fig. 2.
1948 *Globorotalia californica* Cushman & Todd: 96; pl. 16, figs 22, 23.
1950 *Globotruncana* (*Globotruncana*) *stephani* Gandolfi; Reichel: 609; pl. 16, fig. 6; pl. 17, fig. 6.
1953 *Rotundina stephani* (Gandolfi) Subbotina: 165; pl. 2, figs 5–7; pl. 3, figs 1–3.
1954 *Globotruncana stephani* Gandolfi; Ayala-Castanares: 412; pl. 11, fig. 2.
1955 *Globotruncana* (*Rotundina*) *aumalensis* (Sigal); Küpper: 116; pl. 18, fig. 5.
1955 *Globotruncana* (*Rotundina*) *stephani* Gandolfi; Küpper; 116; pl. 18, fig. 6.
1956 *Globotruncana* (*Praeglobotruncana*) *renzi* (Thalmann & Gandolfi) subsp. *primitiva* Küpper: 43; pl. 8, fig. 2a–c.
1957a *Praeglobotruncana stephani* (Gandolfi) Bolli, Loeblich & Tappan: 39; pl. 9, fig. 2.
1959 *Globotruncana kupperi* Thalmann: 130.
1959 *Praeglobotruncana stephani* (Gandolfi); Orlov: text-fig. 687a–c.
1959 *Praeglobotruncana* (*Praeglobotruncana*) *stephani* (Gandolfi); Banner & Blow: 3, text-fig. 1a.
1960a *Praeglobotruncana stephani* (Gandolfi); Klaus: 794; pl. 6, fig. 2a–c.
1961b *Praeglobotruncana stephani* (Gandolfi); Loeblich & Tappan: 284–290; pl. 6, figs 1–8.
1963 *Rotundina stephani* (Gandolfi); Salaj & Samuel: 103–104; pl. 6, figs 2a–c, 3a–c.
1964 *Praeglobotruncana stephani* (Gandolfi); Loeblich & Tappan: C659, fig. 527, 3a–c.
1966 *Praeglobotruncana stephani* (Gandolfi); Eicher: 28; pl. 6, fig. 4.
1966 *Praeglobotruncana stephani* (Gandolfi); Douglas & Slitter: 107; pl. 5, fig. 1a–c; not pl. 4, fig. 1a–c.
1966 *Rotundina stephani* (Gandolfi); Salaj & Samuel: 195; pl. 33, fig. 8.
1967 *Praeglobotruncana stephani* (Gandolfi); Pessagno: 287; pl. 50, figs 9–11.
1969b *Praeglobotruncana stephani* (Gandolfi); Douglas: 173; pl. 2, fig. 1.
1969b *Praeglobotruncana delrioensis* (Plummer); Eicher: 169.
1970 *Praeglobotruncana stephani* (Gandolfi); Eicher & Worstell: 308; pl. 10, fig. 9; pl. 11, figs 2a–c, 3.
1972 *Praeglobotruncana stephani* (Gandolfi); Gawor-Biedowa: 76–78; pl. 8, fig. 1a–c.

REMARKS. This species occurs in the Upper Cenomanian (Zones 11(ii) to 13), and at these levels is often present in substantial numbers. Above the Plenus Marls, in the Lower Turonian, it becomes one of the dominant planktonic species.

In Zone 13 of the Upper Cenomanian the general trend towards increasing ornamentation accelerates and is associated with an increase in height of the spire. Extreme variants are referable to Reichel's (1950) var. *turbinata*, which we include within the synonymy of *P. stephani*. The most important references to *P. stephani* var. *turbinata* are as follows.

1950 *Globotruncana stephani* Gandolfi var. *turbinata* Reichel: 609.
1950 *Globotruncana stephani* Gandolfi var. *turbinata* Reichel; Mornod: 589, text-fig. 17 (1–3); pl. 15, figs 9a–r, 18–20, not 10–17.
1954 *Globotruncana stephani* Gandolfi var. *turbinata* Reichel; Hagn & Zeil: 34; pl. 2, fig. 2; pl. 5, figs 3–4.
1954 *Globotruncana stephani* Gandolfi var. *turbinata* Reichel; Ayala-Castanares: 412; pl. 11, fig. 3.
1956 *Globotruncana* (*Praeglobotruncana*) *stephani* Gandolfi *turbinata* Reichel; Küpper: 43; pl. 8, fig. 1a–c.

1956 *Praeglobotruncana delrioensis* var. *turbinata* (Reichel) Bronnimann & Brown: 532; text-fig. 16c–e.
1957 *Globotruncana* (*Globotruncana* ?) *stephani turbinata* Reichel; Gandolfi: 62; pl. 9, fig. 4.
1960a *Praeglobotruncana stephani* var. *turbinata* (Reichel) Klaus: 795; pl. 6, fig. 3a–c.

Other variants lead to forms related to *P. hagni* and *P. algeriana*. In the upper levels of the Cenomanian all the variants of the *Praeglobotruncana* plexus occur, and the relationships of these species are shown in Fig. 7 (p. 34).

RANGE. Cenomanian Zone 11(ii) to Lower Turonian.

Subfamily **ROTALIPORINAE** Sigal 1958

Genus ***ROTALIPORA*** Brotzen 1942

TYPE SPECIES. *Rotalipora turonica* Brotzen 1942, =*Globorotalia cushmani* Morrow 1934.

Rotalipora cushmani (Morrow 1934)

(Plate 2, fig. 18; Plate 4, figs 7–9)

1934 *Globorotalia cushmani* Morrow: 199; pl. 31, figs 2, 4.
1942 *Rotalipora turonica* Brotzen: 32, text-figs 10, 11 (4).
1945 *Globotruncana alpina* Bolli: 224–225; pl. 9, figs 3, 4.
1946 *Globorotalia cushmani* Morrow; Cushman: 152; pl. 62, fig. 9a–c.
1948 *Globotruncana benacensis* Cita: 147–148; pl. 3, fig. 3a–c.
1948 *Rotalipora cushmani* (Morrow) Sigal: 96; pl. 1, fig. 2; pl. 2, fig. 1.
1950 *Globotruncana* (*Rotalipora*) *montsalvensis* Mornod: 584, text-figs 4 (1), 7 (1, 2).
1950 *Globotruncana* (*Rotalipora*) *montsalvensis* var. *minor* Mornod: 586, text-fig. 8 (1a–c, 2, 4).
1950 *Globotruncana* (*Rotalipora*) *turonica* (Brotzen); Reichel: 607; pl. 16, fig. 5; pl. 17, fig. 5.
1952 *Globotruncana* (*Rotalipora*) *turonica* (Brotzen) var. *expansa* Carbonnier: 118; pl. 6, fig. 4.
1954 *Rotalipora cushmani* (Morrow); Ayala-Castanares: 418; pl. 16, fig. 2.
1954 *Rotalipora turonica* Brotzen; Ayala-Castanares: 422; pl. 14, fig. 2.
1954 *Globorotalia cushmani* Morrow; Frizzell: 129; pl. 20, fig. 28.
1954 *Rotalipora turonica* Brotzen; Hagn & Zeil: 27–28; pl. 1, fig. 5; pl. 4, fig. 4, not fig. 3.
1954 *Rotalipora cushmani* (Morrow); Hagn & Zeil: 29; pl. 1, fig. 3; pl. 4, figs 8–10.
1954 *Rotalipora montsalvensis* Mornod; Hagn & Zeil: 29; pl. 1, fig. 4; pl. 5, fig. 2.
1954 *Rotalipora turonica* subsp. *thomei* Hagn & Zeil: 28; pl. 1, fig. 6; pl. 4, figs 5–6.
1956 *Rotalipora cushmani* (Morrow); Brönnimann & Brown: 537; pl. 20, figs 10–12.
1957 *Rotalipora cushmani* (Morrow); Sacal & Debourle: 58; pl. 25, figs 6–8, 13, 16, 17.
1957a *Rotalipora turonica* Brotzen; Bolli, Loeblich & Tappan: 41; pl. 9, fig. 6a–c.
1957 *Globotruncana* (*Rotalipora*) sp. cf. *G.* (*R.*) *turonica* Brotzen; Edgell: 109; pl. 1, figs 16, 18.
1960a *Rotalipora* (*Rotalipora*) cf. *montsalvensis* var. *minor* Mornod; Klaus: 813–814; pl. 5, fig. 1a–c.
1960a *Rotalipora* (*Rotalipora*) *cushmani* (Morrow); Klaus: 814–815; pl. 5, fig. 2a–c.
1960a *Rotalipora* (*Rotalipora*) *turonica* Brotzen var. *expansa* Carbonnier; Klaus: 815–816; pl. 5, fig. 4a–c.
1961b *Rotalipora cushmani* (Morrow); Loeblich & Tappan: 297–298; pl. 8, figs 1–10.
1964 *Rotalipora montsalvensis* Mornod; Renz, Luterbacher & Schneider: 1089; pl. 7, fig. 1a–c.
1964 *Rotalipora montsalvensis minor* Mornod; Renz, Luterbacher & Schneider: 1089; pl. 7, fig. 2a–c.
1964 *Rotalipora cushmani* (Morrow); Loeblich & Tappan: C659–C661; fig. 528, 1a–c, 2a–c.
1966 *Rotalipora cushmani expansa* (Carbonnier); Salaj & Samuel: 183–184; pl. 12, fig. 7a–c.
1966 *Rotalipora cushmani montsalvensis* (Mornod); Salaj & Samuel: 184; pl. 13, fig. 5a–c.
1966 *Rotalipora cushmani cushmani* (Morrow); Salaj & Samuel: 184–185; pl. 13, figs 2a–c, 4a–c.
1966 *Rotalipora cushmani minor* (Mornod); Salaj & Samuel: 185; pl. 13, fig. 6a–c.
1966 *Rotalipora cushmani thomei* Hagn & Zeil; Salaj & Samuel: 185; pl. 12, fig. 6a–c.
1966 *Rotalipora cushmani turonica* Brotzen; Salaj & Samuel: 185–186; pl. 13, fig. 1a–c; pl. 14, fig. 1a–c.
1967 *Rotalipora cushmani* (Morrow); Pessagno: 292–293; pl. 51, figs 6–9; pl. 101; figs 5–7.
1967 *Rotalipora cushmani* (Morrow); Marks: 272–273; pl. 1, figs 1–12; pl. 2, figs 1–3.
1969b *Rotalipora cushmani* (Morrow); Douglas: 173–174; pl. 1, figs 1–2.
1969 *Rotalipora cushmani* (Morrow); Scheibnerova: 66; pl. 11, figs 2a–c, 5a–c.
1970 *Rotalipora cushmani* (Morrow); Eicher & Worstell: 310, 312; pl. 12, figs 3a–c, 4a–c; pl. 13, fig. 1a–b.
1972 *Rotalipora cushmani cushmani* (Morrow); Gawor-Biedowa: 79–81; pl. 10, figs 1a–c, 2a–c.

REMARKS. This is one of the most conspicuous species of foraminifera in the British Upper Cenomanian. It appears in large numbers in the mid-Cenomanian, while below that level small

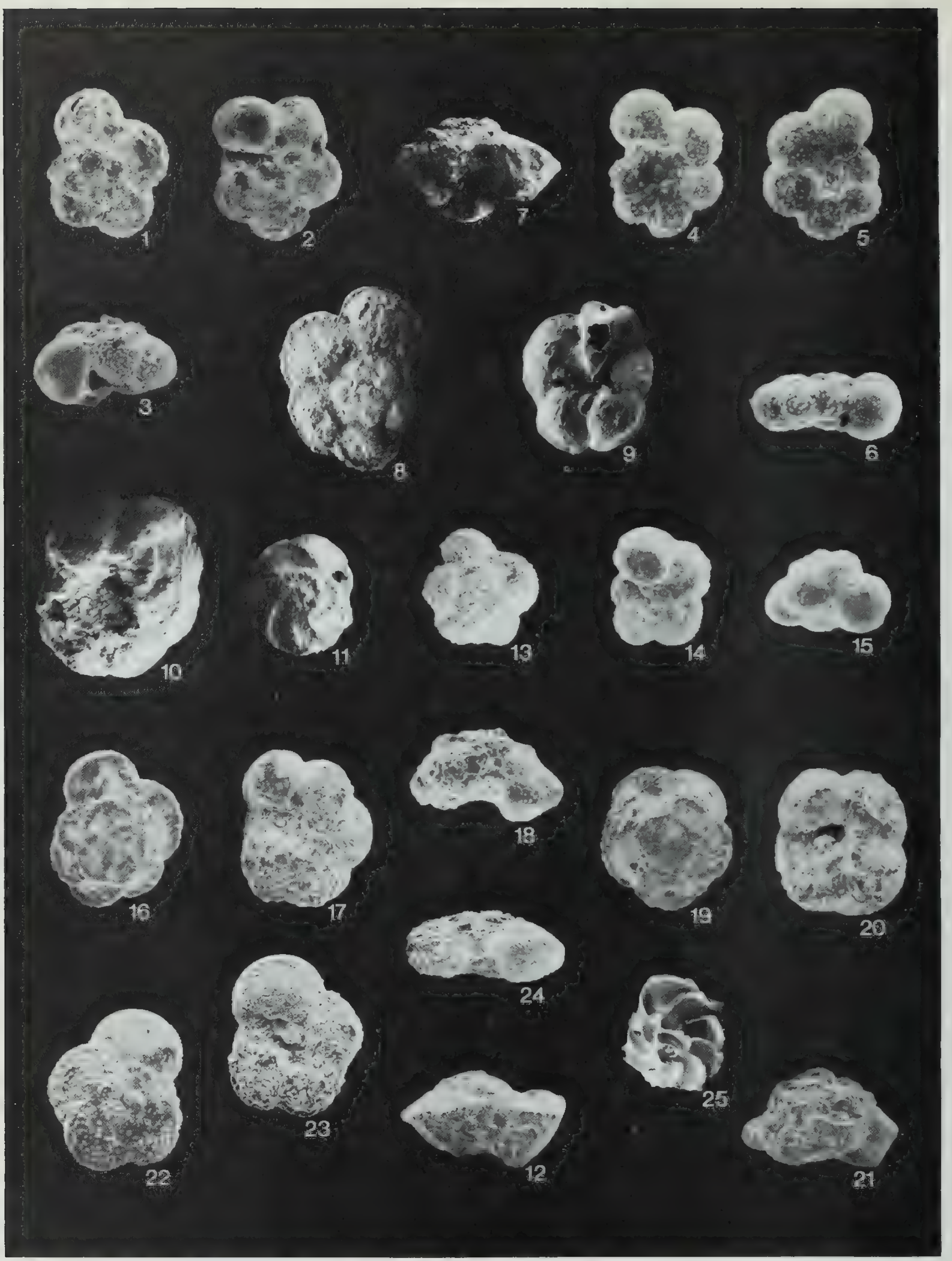
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Plate 4

Figs 1–3 *Hedbergella delrioensis* (Carsey). P 50020. Dorsal, ventral and peripheral views. Upper Cenomanian Zone 14(iia), Bed C, Cenomanian Limestones, Bovey Lane Sandpit, Beer, near Seaton, Devon. × 52.

forms, probably juveniles, occasionally occur. The latter have smooth, inflated chambers, and some individuals show only the slightest trace of a keel. These early representatives are very similar in appearance to *R. evoluta* Sigal and it is possible that this may be the ancestral form of the species. In England the ranges of *R. cushmani* and *R. evoluta* certainly suggest that the former could be derived from the latter. In the Lower Chalk *R. evoluta* is recorded from the lower levels, giving way in the mid-Cenomanian to a population dominated by *R. cushmani*. At no time below this level is *Rotalipora* so dominant an element of the fauna. The overall distribution in the British Isles agrees completely with the scheme of subzones proposed by Pessagno (1967), who divided the Cenomanian into a lower *R. evoluta* Subzone and an upper *R. cushmani*/*R. greenhornensis* (Morrow) Subzone.

An Upper Cenomanian distribution of *R. cushmani* has been recorded by Bandy (1967), Douglas (1969a, b), Eicher (1969b), Eicher & Worstell (1970), Hanzlikova (1961), Klaus (1960a, c), Loeblich & Tappan (1961b), Salaj & Samuel (1963), Scheibnerova (1962) and Zeigler (1957). An account by Marks (1967) showed that *R. cushmani* occurs in some abundance throughout the Craie de Théligny (Sarthe), France. This formation is a lateral equivalent of the upper part of the Grès du Maine (Middle Cenomanian). In the type Cenomanian succession, therefore, *R. cushmani* appears in the upper half of the Middle Cenomanian. Unfortunately the Upper Cenomanian of the type area is composed of the Sables du Perche and the Marnes à Huîtres, and *R. cushmani* has not so far been recorded from these formations, giving no data for the upper limit of the species. Some conclusions can be reached, however, on the basis of the type Turonian succession. This was studied by Butt (1966), and at no level in it has *R. cushmani* been found. In view of this evidence, and the work of one of us (Hart 1975), it must be concluded that *R. cushmani* is restricted to, and characteristic of, the upper half of the Cenomanian. Marks (1967), on the basis of his work on the type Cenomanian, also came to this conclusion, and compared this range with all those previously recorded for the species. The total range of *R. cushmani* has been variously cited within the Middle Cenomanian to Lower Turonian interval, although some authors, e.g. Cushman (1946) and Frizzell (1954), have recorded a range of Lower to Upper Turonian. On the basis of the type Cenomanian succession, as well as the Lower Chalk succession of south-east England, the range is recorded as upper Middle Cenomanian and Upper Cenomanian only.

More recently Salaj & Samuel (1966) have provided data on six subspecies of *R. cushmani*, namely *R. c. cushmani*, *R. c. expansa*, *R. c. thomei*, *R. c. montsalvensis*, *R. c. minor* and *R. c. turonica*. The linear dimensions of all these subspecies, as well as most other characteristics, overlap in range and probably cannot be used for their certain differentiation. Forms like *R. c. minor* have not been encountered by us and the true value of this separation cannot be assessed. Specimens referable to *R. c. thomei* can be found in the Upper Cenomanian of south-east England.

Figs 4–6 *Hedbergella planispira* (Tappan). P 50021. Dorsal, ventral and peripheral views. Upper Albian Zone 6, Bed XIII, Cheriton, Folkestone, Kent. × 27.

Figs 7–9 *Rotalipora cushmani* (Morrow). P 50022–4. Peripheral, dorsal and ventral views. Upper Cenomanian Zone 13, Maiden Newton, Dorset. Fig. 7, ×46; Figs 8, 9, ×48. (See also Pl. 2, fig. 18.)

Figs 10–12 *Rotalipora greenhornensis* (Morrow). Figs 10, 12, P 50026, ×42; Fig. 11, P 50025, ×44. Ventral, dorsal and peripheral views. Upper Cenomanian Zone 13, Maiden Newton, Dorset.

Figs 13–15 *Hedbergella brittonensis* Loeblich & Tappan. P 50027. Dorsal, ventral and peripheral views. Upper Cenomanian Zone 14(iia), Bed C, Cenomanian Limestones, Bovey Lane Sandpit, Beer, near Seaton, Devon. ×50.

Figs 16–21 *Praeglobotruncana stephani* (Gandolfi). Figs 16–18, P 50028–30. Dorsal, ventral and peripheral views. Upper Cenomanian Zone 13, Buckland Newton, Dorset. Figs 19–21, P 50031–3. Specimens referable to the high-spired variant placed by many authors in *P. stephani* var. *turbinata* Reichel. Dorsal, ventral and peripheral views. Upper Cenomanian Zone 13, Beachy Head, near Eastbourne, Sussex. Fig. 16, ×45; Fig. 17, ×57; Fig. 18, ×61; Figs 19, 20, ×48; Fig. 21, ×67.

Figs 22–24 *Praeglobotruncana delrioensis* (Plummer). P 50034. Dorsal, ventral and peripheral views. Middle Cenomanian Zone 10, Beachy Head, near Eastbourne, Sussex. ×72.

Fig. 25 *Epistomina spinulifera* (Reuss). P 50038. Dorsal view. Middle Albian Zone 4, Bed VII, Copt Point, Folkestone, Kent. ×19.

This was initially described by Hagn & Zeil (1954) as a variety of the parent species. In large populations, however, even this form merges with the variations included in the original species.

RANGE. Rare, primitive forms are encountered in the lower part of the Middle Cenomanian, but large numbers of typical individuals appear only above the mid-Cenomanian non-sequence, dominating Zones 11(ii), 12, 13 and 14(i–iia) (Plenus Marls Beds 1–3). The species does not range above the Cenomanian Stage.

Rotalipora evoluta Sigal 1948
(Plate 3, figs 13–15)

1940 *Globorotalia delrioensis* Plummer; Tappan: 123; pl. 19, fig. 14.
1946 *Globorotalia delrioensis* Plummer; Loeblich & Tappan: 257, text-fig. 4B.
1948 *Rotalipora cushmani* var. *evoluta* Sigal: 100; pl. 1, fig. 3; pl. 2, fig. 2.
1948 *Globorotalia almadenensis* Cushman & Todd: 98; pl. 16, fig. 24.
1950 *Globotruncana* (*Rotalipora*) *appenninica* Renz; Mornod: 579–582 (part), text-fig. 3 (1a–c, 2a–c, not 3a–c), text-fig. 4 (not 3a–c, ? 4a–c), text-fig. 5 (not 1a–c); pl. 15, fig. 1a–c.
1951 *Globotruncana appenninica* cf. *alpha* Gandolfi; Bolli: 193; pl. 34, figs 1–3.
1952 *Globotruncana* (*Rotalipora*) *appenninica* Renz var. *typica* Gandolfi; Bolli *in* Church: 69, text-fig. 2.
1955 *Globotruncana* (*Rotalipora*) *evoluta* (Sigal) Küpper: 115; pl. 18, fig. 3a–c.
1955 *Globotruncana* (*Rotalipora*) *appenninica appenninica* Renz; Küpper: 114; pl. 18, fig. 2a–c.
1957a *Rotalipora* cf. *appenninica* (Renz); Bolli, Loeblich & Tappan: 41; pl. 9, fig. 5a–c.
? 1960a *Rotalipora* (*Thalmanninella*) *evoluta* (Sigal); Klaus: 810; pl. 4, fig. 3a–c.
1961b *Rotalipora evoluta* Sigal; Loeblich & Tappan: 298–299; pl. 7, figs 1–4.
1961b *Rotalipora greenhornensis* (Morrow); Loeblich & Tappan: 299–301 (part); pl. 7, figs 5, 6, not 7–10.
non 1962 *Rotalipora evoluta* Sigal; Ayala-Castanares: 26–27; pl. 4, fig. 2a–c; pl. 10, fig. 3a–c.
1964 *Rotalipora* cf. *appenninica evoluta* Sigal; Renz, Luterbacher & Schneider: 1088; pl. 8, fig. 3a–c.
non 1964 *Rotalipora evoluta* Sigal; Todd & Low: 46; pl. 2, fig. 3a–c.
1966 *Thalmanninella evoluta* (Sigal); Salaj & Samuel: 179–180; pl. 11, fig. 3a–c; pl. 12, fig. 2a–c.
1967 *Rotalipora evoluta* Sigal; Pessagno: 294–295; pl. 49, figs 12–14; pl. 53, figs 6–8; pl. 98, fig. 12.

REMARKS. This species differs from *R. appenninica* (Renz) in being about half as large and in having more angular chambers. It also possesses a more prominent umbilical shoulder than any other species in the genus. *R. evoluta* characterizes the lower part of the Lower Chalk succession and is probably ancestral to all later species of *Rotalipora*.

Loeblich & Tappan (1961b) do not give a range for *R. evoluta* in European terms, but they list the Grayson Formation as one of its more important levels of occurrence. This formation is covered by Pessagno's (1967) *R. evoluta* Subzone. However, Bandy (1967: text-fig. 7) does not agree with this range. He considers the *Rotalipora* group to have derived from *Ticinella* Reichel 1950 in the Upper Albian and *R. appenninica balernaensis* Gandolfi to be the origin for the whole plexus. *R. evoluta*, according to Bandy, was derived from *R. greenhornensis* (Morrow), and thus it must be restricted to the Upper Cenomanian. *R. evoluta* then in turn developed *R. reicheli* Mornod and *R. cushmani*. Although this evolutionary sequence more nearly agrees with the results of Klaus (1960a), it contradicts the range of *R. evoluta* as found by us. However, Salaj & Samuel (1966) use *Thalmanninella evoluta* as an indicator for the lowest part of a three-fold division of the Cenomanian.

Thus there is some variance of opinion as to the range of this species. However, in regions as far apart as Texas, the Carpathians, the Pacific Ocean, the North Atlantic Ocean and south-east England, *R. evoluta* can be used as a Lower Cenomanian indicator.

RANGE. Lower Cenomanian Zones 7–10, and Middle Cenomanian Zone 11(i).

Rotalipora greenhornensis (Morrow 1934)
(Plate 4, figs 10–12)

1934 *Globorotalia greenhornensis* Morrow: 199; pl. 39, fig. 1.

1940 *Planulina greenhornensis* (Morrow) Cushman: 37; pl. 7, fig. 1.
1946 *Planulina greenhornensis* (Morrow); Cushman: 159; pl. 65, fig. 3a–c.
1948 *Rotalipora globotruncanoides* Sigal: 100; pl. 1, fig. 4; pl. 2, figs 3–5.
1948 *Thalmanninella brotzeni* Sigal: 102; pl. 1, fig. 5; pl. 2, figs 6–7.
1948 *Globorotalia decorata* Cushman & Todd: 97; pl. 16, fig. 21.
1950 *Globotruncana (Rotalipora) appenninica* Renz var. *typica* Gandolfi; Mornod: 582; text-fig. 9.2a–c.
non 1950 *Globotruncana (Thalmanninella) brotzeni* Sigal; Mornod: 586; text-fig. 9.1a–c.
1952 *Rotalipora globotruncanoides* Sigal; Sigal: 26; text-fig. 24.
1953 *Rotalipora appenninica* (Renz); Subbotina: 159 (part); pl. 1, fig. 8a–c, not figs 5a–c, 6a–c, 7a–c; not pl. 2, figs 1a–c, 2a–c.
1954 *Rotalipora globotruncanoides* Sigal; Hagn & Zeil: 23–25; pl. 4, fig. 7.
non 1955 *Globotruncana (Rotalipora) globotruncanoides* Sigal; Küpper: 113; pl. 18, fig. 1a–c.
1955 *Globotruncana (Thalmanninella)* sp. Küpper: 115; pl. 18, fig. 4a–c.
? 1956 *Globotruncana* n. sp., indet. Küpper: 44; pl. 8, fig. 3a–c.
1956 *Thalmanninella greenhornensis* (Morrow) Brönnimann & Brown: 535; pl. 20, figs 7–9.
1957 *Globotruncana (Rotalipora) appenninica appenninica* Renz; Gandolfi: 60; pl. 9, fig. 2.
1957 *Rotalipora globotruncanoides* Sigal; Sacal & Debourle: pl. 25, ? fig. 1, fig. 3, ? fig. 11, ? fig. 15.
non 1957a *Rotalipora brotzeni* (Sigal); Bolli, Loeblich & Tappan: 41; pl. 9, fig. 7a–c.
non 1959 *Rotalipora globotruncanoides* Sigal; Banner & Blow: pl. 2, fig. 4.
1960a *Rotalipora (Thalmanninella) greenhornensis* (Morrow) Klaus: 805; pl. 2, fig. 3a–c.
? 1960a *Rotalipora (Thalmanninella) brotzeni* Sigal; Klaus: 805; pl. 3, fig. 1a–c.
1961b *Rotalipora greenhornensis* (Morrow); Loeblich & Tappan: 299–301 (part); pl. 7, figs 7–9, not figs 5–6, 10.
1962 *Rotalipora greenhornensis* (Morrow); Ayala-Castanares: 28–30; ? pl. 5, fig. 3a–c; pl. 10, fig. 3a–b.
1964 *Rotalipora greenhornensis* (Morrow); Loeblich & Tappan: C659–C661 (part), fig. 528, 4a–c, not 3a–c.
1965 *Rotalipora greenhornensis* (Morrow); Eicher: 906; pl. 106, fig. 11.
1966 *Thalmanninella greenhornensis* (Morrow); Salaj & Samuel: 180, text-fig. 15a–b.
? 1966 *Thalmanninella deeckii* (Franke); Salaj & Samuel: 179; pl. 12, fig. 4a–c.
1966 *Rotalipora tehamaensis* Marianos & Zingula: 339; pl. 38, fig. 4a–c.
1967 *Rotalipora greenhornensis* (Morrow); Pessagno: 295–297; pl. 50, fig. 3; pl. 51, figs 13–21; pl. 101, figs 3–4.
1969b *Rotalipora greenhornensis* (Morrow); Douglas: 174; pl. 1, fig. 3.
1970 *Rotalipora greenhornensis* (Morrow); Eicher & Worstell: 312; pl. 12, fig. 2a–c; pl. 13, fig. 3a–b.
1972 *Rotalipora greenhornensis* (Morrow); Gawor-Biedowa: 83–84; pl. 9, figs 4–5.

REMARKS. This species shows raised, beaded sutures on both the spiral and umbilical sides. The chambers of the final whorl do not increase so rapidly in size as in other members of the genus. However, the marked umbilical shoulders and the raised sutures relate this form to *R. evoluta* and it is likely that *R. greenhornensis* is an Upper Cenomanian derivative of the former species. Bandy (1967) deduces a reversed relationship although Pessagno (1967) came to the same conclusions as we do. Loeblich & Tappan (1961b) figured hypotypes from the Greenhorn Formation, Hartland Shale Member, and these are remarkably similar to the specimens found in England. Eicher (1969b) records *R. greenhornensis* from the Greenhorn Formation of the western interior of the United States, indicating that it extends up as far as the Cenomanian/Turonian boundary. *R. cushmani* is also recorded in the same sequences, and while it has a closely similar range, at a few localities it extends further up the succession. In England *R. cushmani* appears earlier in the succession than *R. greenhornensis* but this may be due to several external controls; *R. greenhornensis* is more abundant in more southerly areas, so this disparity in the recorded ranges is not thought to be significant. Klaus (1960a, c) gives the range in Switzerland as Middle to Upper Cenomanian, which is not radically different from that in the British Isles. Douglas (1969b : text-fig. 4) places *R. greenhornensis* in the Upper Cenomanian and extends its range downwards slightly into the Lower Cenomanian.

As was suggested by Pessagno (1967), there is a possibility that *R. greenhornensis* is a junior synonym of *Rotalipora deeckii* (Franke 1925 : 88–90; pl. 8, fig. 7a–c). The type figures of Franke's species indicate its closeness to *R. greenhornensis*. Many European workers, more familiar with Franke's species, retain the two as separate entities. One of the latest references to *Thalmanninella deeckii* has been included in the synonymy.

RANGE. Cenomanian Zones 11(ii)–14(i) (Plenus Marls Bed 1).

Family **GLOBOTRUNCANIDAE** Brotzen 1942

Genus ***GLOBOTRUNCANA*** Cushman 1927

TYPE SPECIES. *Pulvinulina arca* Cushman 1926.

Globotruncana cf. ***indica*** (Pessagno 1967)

(Plate 3, figs 7–9)

? 1955 *Globotruncana indica* Jacob & Sastry; Gandolfi: 19; text-fig. 4, 3a–b.
1967 *Marginotruncana indica* Pessagno: 307; pl. 55, figs 3, 8–10; pl. 57, figs 6–9; pl. 98, fig. 2 (non Jacob & Sastry 1950).

REMARKS. In the upper levels of the Plenus Marls (Zone 14) rare specimens of *Globotruncana* have been found. They have been referred tentatively to *G. indica*, as described by Pessagno (1967), on the basis of the flat dorsal side and slightly inflated chambers on the ventral surface. The aperture, unlike the extraumbilical aperture of *Praeglobotruncana*, is almost umbilical, and often displays globotruncanid apertural flaps. The suggested evolution of these early globotruncanids, from *P. delrioensis* through *P.* cf. *hagni*, is indicated in Fig. 7 (p. 34). *G.* cf. *indica* is the earliest *Globotruncana* known from the British Cretaceous. Its appearance in the upper levels of the Plenus Marls (Beds 4–8), and in the upper levels of Bed C of the Cenomanian Limestones (Smith 1957a, etc.) in the south-west of England, is of major importance in the definition of the Cenomanian/Turonian boundary. Many workers regard *Globotruncana* as typical of the Turonian to Senonian interval.

RANGE. The complete range of this species is unknown, and only its first appearance is recorded here. Although rare specimens have been found in the upper levels of the Plenus Marls (Zone 14(iia)), only in the Middle Chalk can large numbers be found.

Superfamily **CASSIDULINACEA** d'Orbigny 1839

Family **ANOMALINIDAE** Cushman 1927

Subfamily **ANOMALININAE** Cushman 1927

Genus ***GAVELINELLA*** Brotzen 1942

TYPE SPECIES. *Discorbina pertusa* Marsson 1878.

Gavelinella baltica Brotzen 1942

(Plate 1, figs 36–38)

1942 *Gavelinella baltica* Brotzen: 50; pl. 1, fig. 7.
1962 *Gavelinella baltica* Brotzen; Jefferies: pl. 78, fig. 9a–c.
1962 *Gavelinella baltica* Brotzen; Hiltermann & Koch: 319; pl. 47, fig. 1.
1972 *Gavelinella (Gavelinella) baltica* Brotzen; Gawor-Biedowa: 125–126; pl. 17, fig. 5a–c.

REMARKS. This species is very similar to *G. intermedia* (Berthelin), from which it differs in the inflation of the final three chambers. *G. baltica* develops (Fig. 8) from *G. intermedia* in the Upper Albian, although typical forms are seen only in the Cenomanian. These earlier, more primitive, forms were described as *Anomalina rudis* (Reuss) by Chapman (1898).

RANGE. Cenomanian Zones 7–14(i) (Plenus Marls Bed 1). Rare, primitive forms have however been found in Albian/Cenomanian Zone 6a.

Gavelinella cenomanica (Brotzen 1942)

(Plate 1, figs 27, 28)

1942 *Cibicidoides (Cibicides) cenomanica* Brotzen: 54; pl. 2, fig. 2a–c.

1954 *Anomalina (Pseudovalvulineria) cenomanica* (Brotzen) var. *cenomanica* Vasilenko: 87; pl. 9, fig. 2.
1957 *Gavelinopsis cenomanica* (Brotzen) Hofker: 321, text-fig. 370.
1962 *Gavelinopsis cenomanica* (Brotzen); Hiltermann & Koch: 318; pl. 48, fig. 1.
1966 *Gavelinopsis cenomanica* (Brotzen); Michael: 436; pl. 50, figs 16–17.
1972 *Gavelinella (Gavelinella) cenomanica* (Brotzen) Gawor-Biedowa: 126–128; pl. 17, fig. 4a–c.

Remarks. This species differs from *G. intermedia* in having a more or less marked rim around the umbilicus. There has been confusion as to the generic position of this species, attributable to the

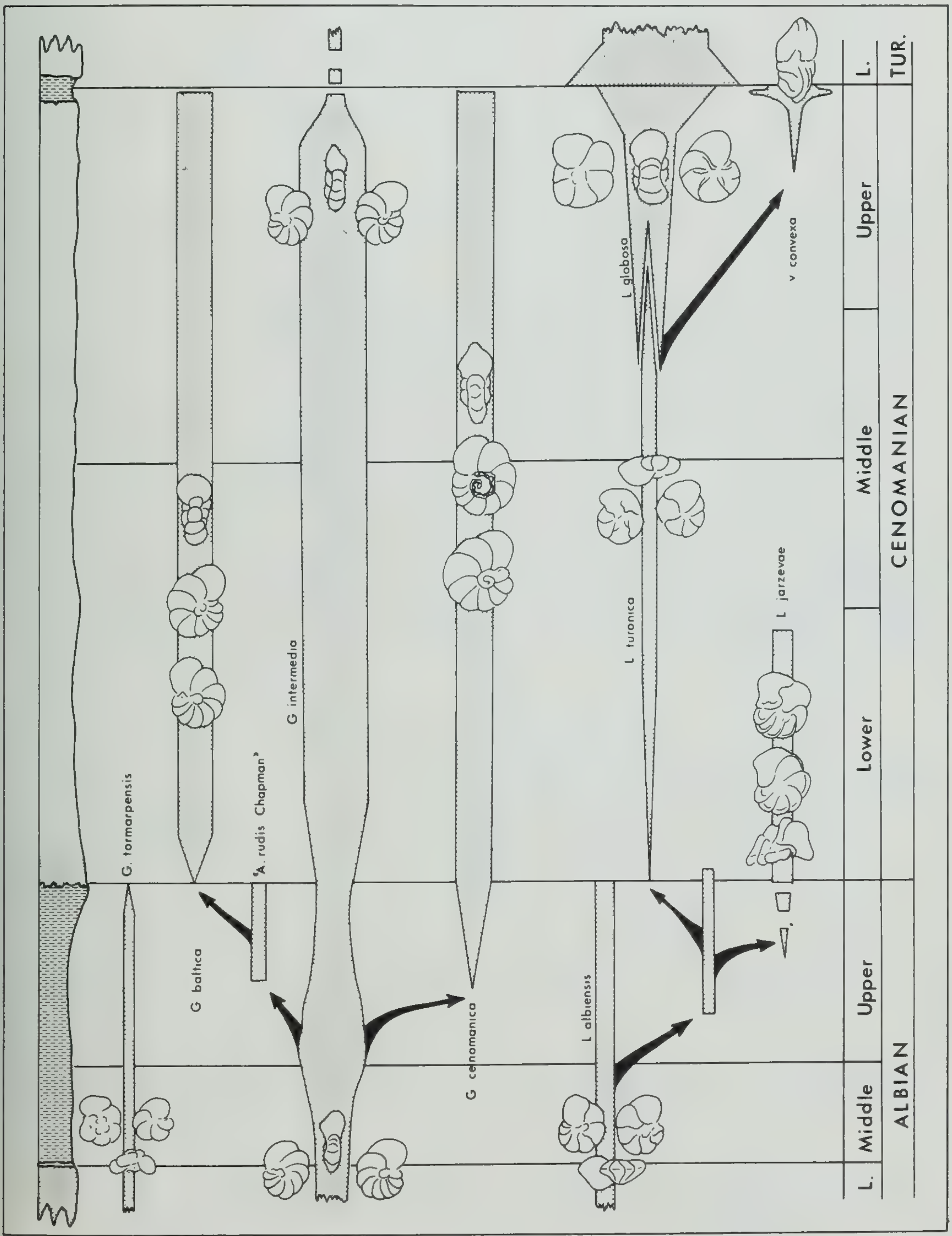

G. tormarpensis
G baltica
'A. rudis Chapman'
G intermedia
G cenomanica
L albiensis
L turonica
L globosa
v convexa
L jarzevae
L.
Middle
Upper
Lower
Middle
Upper
L.
ALBIAN
CENOMANIAN
TUR.

Fig. 8 Evolution of the *Gavelinella* and *Lingulogavelinella* groups.

initial description of Brotzen. In his 1942 account he calls the species *Cibicidoides* (*Cibicides*) *cenomanica*, and *Cibicides cenomanica* in the plate explanation. Hofker (1957) placed the species in *Gavelinopsis*. However, an examination of the wall structure has shown that there is a double septal wall which is in agreement with the generic description of *Gavelinella*. *G. cenomanica* can be shown, by a series of transitional forms, to have evolved from *G. intermedia* in the Upper Albian. Fuchs (1967) records specimens of *G. intermedia* from the Albian of Holland, but figures (Fuchs 1967 : fig. 6a) a specimen showing a slight trace of the umbilical rim which is characteristic of *G. cenomanica*. Fuchs' specimens presumably were from a level where this transition was already well advanced.

RANGE. While primitive forms are found in Albian Zones 5–6, this species is commonly found in Albian/Cenomanian Zone 6a and Cenomanian Zones 7–14(iia) (Plenus Marls Beds 2 and 3).

Gavelinella intermedia (Berthelin 1880)

(Plate 1, figs 33–35)

1880 *Anomalina intermedia* Berthelin: 67; pl. 4, fig. 14a–b.
1898 *Anomalina ammonoides* Reuss; Chapman: 3; pl. 1, fig. 4.
1942 *Gavelinella intermedia* (Berthelin) Brotzen: 52, text-fig. 18.
1954 *Gavelinella intermedia* (Berthelin); Bartenstein: 49; pl. 1, figs 21–28.
1954 *Anomalina* (*Anomalina*) *suturalis* Mjatliuk; Vasilenko: 51; pl. 1, fig. 1.
1954 *Anomalina* (*Anomalina*) *hostaensis* Morosowa; Vasilenko: 52; pl. 1, fig. 3.
1954 *Anomalina* (*Anomalina*) *infracomplanata* Mjatliuk; Vasilenko: 53; pl. 1, fig. 4.
1957 *Gavelinella intermedia* (Berthelin); Hofker: 285–286, text-figs 336–337.
1960 *Gavelinella intermedia* (Berthelin); Moullade: 138; pl. 2, figs 15–17.
1960 *Gavelinella flandrini* Moullade: 137; pl. 2, figs 10–14.
1965 *Gavelinella intermedia* (Berthelin); Neagu: 32; pl. 8, figs 1–2.
1965 *Gavelinella* (*Berthelina*) *intermedia* (Berthelin); Malapris: 138–139; pls 1, 2, 5, including forms placed in *G. reussi* (Khan).
1972 *Gavelinella* (*Berthelina*) *intermedia* (Berthelin); Gawor-Biedowa: 120–122; pl. 15, figs 7–9; text-fig. 12.

REMARKS. Berthelin's specimens were from the Gault Clay of Montcley. The species ranges through both the Albian and the Cenomanian. It is very variable in appearance, and two off-shoots from the main lineage gave rise to *G. baltica* and *G. cenomanica* in the Upper Albian.

RANGE. Albian Zone 3 to Cenomanian Zone 14(iia) (Plenus Marls Bed 3).

Gavelinella tormarpensis Brotzen 1942

(Plate 1, figs 31–32)

1942 *Gavelinella tormarpensis* Brotzen: 52; pl. 1, fig. 6.
1965 *Gavelinella tormarpensis* Brotzen; Malapris: 148; pl. 3, figs 1–4.

REMARKS. This very small, rounded species is one of the earliest members of the *Gavelinella* plexus recorded from the Gault Clay succession. Although common in the Middle Albian (up to Zone 4a) only rare occurrences have been reported from the Upper Albian. Specimens from south-east England are identical with specimens figured by Malapris from the type Albian.

Small specimens very closely similar to this species are recorded from the Cenomanian and Turonian, but at these higher levels a small boss or plug in the centre of the specimen gives a slightly domed appearance to the dorsal side. These individuals are probably referable to *Gavelinella minima* (Vieaux).

RANGE. Although known from the Lower Albian (Aube, France), this species has been mainly recorded from the Middle Albian Zones 3–4a. Rare specimens also have been recorded from the Upper Albian.

Genus ***LINGULOGAVELINELLA*** Malapris 1965

TYPE SPECIES. *Lingulogavelinella albiensis* Malapris 1965.

Lingulogavelinella globosa (Brotzen 1945)
(Plate 1, figs 12–14)

1945 *Anomalinoides globosa* Brotzen: 58; pl. 2, fig. 6a–c.
1962 *Anomalinoides globosa* Brotzen; Jefferies: 78; fig. 19a–c.
1966 *Orostella turonica* Butt: 180; pl. 3, fig. 6; pl. 4, fig. 4.
1972 *Lingulogavelinella globosa* (Brotzen) Gawor-Biedowa: 107–108; pl. 15, figs 4a–c, 5a–c.

REMARKS. A study of material from the type Turonian shows that Butt's (1966) new species *O. turonica* is identical with that described as *A. globosa* by Brotzen (1945). The new genus *Orostella*, erected by Butt to include his new species and *L. globosa*, falls within the definition of *Lingulogavelinella* Malapris (1965 : 139), so *Orostella* Butt is suppressed as a junior synonym.

L. globosa is a distinctive foraminifer, recognized by the apertural flaps which cover the edges of the chambers on the ventral side, forming a star-shaped pattern. It is represented by small, atypical, forms in the Upper Cenomanian, while more characteristic individuals appear above the Cenomanian/Turonian boundary – especially in the section along the Cher Valley, Touraine, France.

RANGE. Rare in the Upper Cenomanian Zone 13, becoming more abundant in Beds 1–3 of the Plenus Marls (Zone 14(i)–(ii)). Above this level *L. globosa* is an important element of the fauna.

Lingulogavelinella globosa (Brotzen) var. ***convexa*** nov.
(Plate 1, figs 24–26)

1962 *Pseudovalvulineria* sp. Jefferies: pl. 78, fig. 15a–c.

DERIVATION OF NAME. The ventral side of this variety is strongly convex whereas the dorsal side can be either flat or slightly convex.

DIAGNOSIS. Similar to *L. globosa*, but strongly convex ventrally.

DETERMINATION. Test free, trochospiral and planoconvex; involute, dorsal side flat or very slightly convex, generally with 6 to 7 chambers in the final whorl visible. Convex ventral side also only displaying the last whorl. Unlike in *L. globosa* the margin of the test subangular instead of rounded. Chambers of the final whorl slightly inflated dorsally, increasing gradually in size. Sutures distinct and radial on both sides. Walls calcareous, perforate, granular, bilamellar, but usually recrystallized. Apertural flaps prominent in the final whorl and characteristic of the variety as well as the typical species.

DIMENSIONS. Average diameter 0·46 mm; average thickness 0·19 mm.

REMARKS. This variety is very similar indeed to *L. globosa*, but sufficiently distinct to warrant its elevation as a variety. Although it is superficially distinct its restricted occurrence indicates it may be an ecophenotypic variant. Several variants have been found at other very restricted stratigraphic levels, although none have any diagnostic value.

RANGE. Very rare in the Upper Cenomanian Zone 13, abundant only in Bed 1 of the Plenus Marls (Zone 14(i)).

Lingulogavelinella jarzevae (Vasilenko 1954)
(Plate 1, figs 29–30)

? 1945 *Cibicides formosa* Brotzen: 55; pl. 2, fig. 3a–c.
1954 *Cibicides* (*Cibicides*) *jarzevae* Vasilenko: 121; pl. 17, fig. 3a–c.
? 1972 *Lingulogavelinella formosa* (Brotzen) Gawor-Biedowa: 105–106; pl. 14, fig. 1a–c; text-fig. 7.

REMARKS. This distinctive species is recognized by the totally flat spiral side and the strongly elevated umbilical side. It may be the same as Brotzen's *Cibicides formosa*.

RANGE. While rare, immature specimens have been found in the Upper Albian Zones 5a–6, this species is abundant in Albian/Cenomanian Zone 6a and the Lower Cenomanian Zones 7–9. In the Lower Chalk of the south-east of England rare specimens have also been recorded from the base of the overlying Zone 10 and from a thin band near the top of Zone 10, just below the Zone 10/Zone 11(i) boundary. It is probably an indicator of shallow-water conditions.

Superfamily **ROBERTINACEA** Reuss 1855

Family **CERATOBULIMINIDAE** Cushman 1927

Subfamily **CERATOBULIMININAE** Cushman 1927

Genus ***CONORBOIDES*** Hofker *in* Thalmann 1952

TYPE SPECIES. *Conorbis mitra* Hofker 1951.

Conorboides lamplughi (Sherlock 1914)

(Plate 1, figs 21–23)

1914 *Pulvinulina lamplughi* Sherlock: 290; pl. 19, fig. 16.
1933a *Discorbis turbo* Eichenberg: 20; pl. 1, fig. 11 (non d'Orbigny).
1950 *Lamarckina lamplughi* (Sherlock) ten Dam: 49, text-fig. 5.
1965 *Lamarckina lamplughi* (Sherlock); Neagu: 34; pl. 9, figs 6, 7.

REMARKS. Both ten Dam and Neagu place this species in the genus *Lamarckina* Berthelin. It is however very similar to *C. mitra*, and here it is referred to *Conorboides* Hofker *in* Thalmann.

RANGE. Rare in Middle Albian Zone 3.

Subfamily **EPISTOMININAE** Wedekind 1937

Genus ***EPISTOMINA*** Terquem 1883

TYPE SPECIES. *Epistomina regularis* Terquem 1883.

Epistomina spinulifera (Reuss 1862)

(Plate 4, fig. 25)

1862 *Rotalia spinulifera* Reuss: 93; figs 3a–5c.
1883 *Epistomina spinulifera* (Reuss) Uhlig: 768; pl. 7, figs 5–7.
1896 *Pulvinulina spinulifera* (Reuss) Chapman: 9; pl. 2, fig. 1a–c.
1933a *Rotalia polypoides* Eichenberg: 21; pl. 3, fig. 1a–c.
1933b *Epistomina spinulifera* (Reuss); Eichenberg: 192; pl. 22, fig. 1a–d.
1947 *Epistomina spinulifera* (Reuss); ten Dam: 28–29, figs 7a–c.
1948b *Epistomina spinulifera* (Reuss); ten Dam: 170; pl. 2, fig. 5.
1954 *Brotzenia spinulifera* (Reuss) Hofker: 182–183, text-figs 9–12.
1963 *Brotzenia spinulifera* (Reuss); Cordey: 655–656.

REMARKS. This easily recognized species characterizes the greater part of the Lower Gault Clay sequence of south-east England. The ornamentation is quite variable and a study of this feature reveals the sequence outlined below.

RANGE. This species is first recorded from Zone 2 of the Middle Albian and it extends, with increasingly strong ornamentation, through to Zone 4, where at its acme of development specimens are commonly quite massive. In Zone 4a there is some degeneration, and it is not usually recorded above that zone. Reworked material is occasionally found at higher levels in the Gault Clay succession.

Genus ***HOEGLUNDINA*** Brotzen 1948

TYPE SPECIES. *Rotalia elegans* d'Orbigny 1826.

Hoeglundina carpenteri (Reuss 1862)

(Plate 1, figs 15–17)

1862 *Rotalia carpenteri* Reuss: 94; pl. 13, fig. 6a–c.
1898 *Pulvinulina carpenteri* (Reuss) Chapman: 8; pl. 1, fig. 11a–c.
1948b *Epistomina carpenteri* (Reuss) ten Dam: 165; pl. 1, fig. 4.

1950 *Epistomina carpenteri* (Reuss); ten Dam: 50; pl. 4, fig. 3.
1954 *Hoeglundina carpenteri* (Reuss) Hofker: 104–105; text-figs 36–37.
1965 *Epistomina carpenteri* (Reuss); Neagu: 34; pl. 9, figs 3–4.

REMARKS. This is a very variable species, including individuals with a smooth test and ranging through to those with small spines on the chamber surfaces.

RANGE. Middle Albian Zones 3–4.

Hoeglundina chapmani (ten Dam 1948)
(Plate 1, figs 18–20)

1860 *Rotalia elegans* d'Orbigny; Jones & Parker: pl. 20, fig. 46.
1898 *Pulvinulina carcolla* (Roemer); Chapman: 7; pl. 1, fig. 9.
1898 *Pulvinulina elegans* (d'Orbigny) Chapman: 6; pl. 1, fig. 8.
1933a *Epistomina elegans* (d'Orbigny) Eichenberg: 22; pl. 7, fig. 1.
1948b *Epistomina chapmani* ten Dam: 166; pl. 1, fig. 5a–c.
1950 *Epistomina chapmani* ten Dam; ten Dam: 453; pl. 4, fig. 6.
1954 *Hiltermannia chapmani* (ten Dam) Hofker: 191–193, text-figs 27–32.
1965 *Epistomina chapmani* ten Dam; Neagu: 34; pl. 9, fig. 5.

REMARKS. Hofker (1954) separated *Hiltermannia* (type species *H. chapmani*) from *Hoeglundina* on the basis of its smaller internal partitions. Loeblich & Tappan (1964) suggested that the relative size of these features is a specific character. Cordey (1963), for the same reason, rejected Hofker's separation of the genera *Epistomina* and *Voorthuysenia* Hofker.

RANGE. Middle Albian Zones 3–4a.

Foraminiferal zonations

A preliminary foraminiferal distribution chart for the mid-Cretaceous was published in Bruckshaw *et al.* (1961 : fig. 14). While this was based on a single section (Shakespeare Cliff borehole, Dover), it was nevertheless the first completely microfaunal subdivision of the Aptian to Turonian interval in the British Isles. The zonal numbers used in the present account are based on that previous work, and because of this, only Zones 3–14 are used here. Zones 1 and 2 (a and b) refer to the Atherfield Clay and the Lower Greensand. The original distribution chart was included in a report on the Channel Tunnel Survey. Since then a second, more exhaustive, site investigation has been undertaken, and this, together with the subsequent research, has changed many of the views then held. The zonation, as used in this account, encompasses the Gault Clay (Middle and Upper Albian), the Lower Chalk (Cenomanian, approximately) and the lower levels of the Middle Chalk (Turonian).

According to Kulp (1961) this stratigraphic interval covers approximately 30 Ma, of which 20 Ma is occupied by the Cenomanian. This has been criticized as excessively long by Rubinshtein (1963) and also by Casey (*in* Harland *et al.* 1964). Rubinshtein based his objections on the thickness of sediment involved, while Casey argued that the Cretaceous should be divided into stages of equal duration. The idea that the Cenomanian Stage could occupy 20 Ma of the 72 Ma (135–63 Ma) available for the whole Cretaceous prompted Bandy (1967) to suggest that it would be more appropriate to divide the Cretaceous into three major units, instead of the more customary two. In this tripartite scheme the Cenomanian would constitute the Middle Cretaceous Substage. Whichever system of subdivision is adopted, the delimitation of the Cenomanian is of prime importance, as its base would be either the base of the Upper Cretaceous (following previous workers) or the base of the Middle Cretaceous (following Bandy).

The value of planktonic foraminifera for correlation has been discussed at length by Bandy (1964, 1967). In the Upper Cretaceous, and even more in the Cenozoic, there is such a variety of planktonic foraminifera that it has been possible to formulate accurate zonations based on this group. In the Lower Cretaceous, however, there are few genera and species which can be used for correlation. In most cases these belong to primitive, long-ranging groups. While this is true of the Albian, there are changes in the Cenomanian, when planktonic foraminiferal evolution began to accelerate, and this continued throughout the Cenomanian with the appearance of more typically Upper Cretaceous lineages. The rapid diversification of planktonic foraminifera during the Cenomanian, however, does not allow the identification of more than two zones. The Albian cannot, at the present time, be divided into zones and a single population identifies it.

Because of the deficiency in planktonic foraminifera, benthonic species have been used in conjunction with them in the compilation of another zonal scheme for local correlation. This, permitting correlation within the Anglo-Paris Basin, can be compared with other more distant successions on the basis of its planktonic content. Apart from the preliminary zonal scheme of 1961, which also was based on both benthonic and planktonic species, there has been no attempt at a comprehensive microfaunal analysis of the mid-Cretaceous in Great Britain. Only two previous works, Williams-Mitchell (1948) and Barnard & Banner (1953), were concerned with correlation, although others, e.g. Chapman (1891–98), Barr (1962), have documented the fauna from selected horizons. Unfortunately both used previously-defined macropalaeontological zones as a foundation and neither produced a workable system of microfaunal subdivision. It is likely that this lack of success deterred further attempts at a solution of this problem. The present authors' approach has been to collect samples at regular intervals throughout the succession under investigation, without reference to any other faunal controls. The result has been the detection of the actual microfaunal boundaries, which can now be related to any macrofaunal scheme produced for the same sequence.

a. Planktonic zonal scheme

Williams-Mitchell (1948), in his analysis of the zonal value of the foraminifera, used benthonic species primarily, although two planktonic species (*Globigerina portsdownensis* Williams-Mitchell and *Rotalipora turonica* Brotzen) were described from the Cenomanian. This is the only use made of planktonic foraminifera in the British mid-Cretaceous to date. Although the paucity of genera allows the identification of only four zones, these nevertheless can be used for international correlation. The planktonic species involved, and the zonal analysis, are shown in Fig. 9.

(i) *Hedbergella delrioensis/H. infracretacea* Zone – Middle & Upper Albian.

Type section: Shakespeare Cliff Borehole, Dover, 1958 (544′0″ (base of Lower Gault Clay) to 403′1″) (165·81–122·86 m).

Hedbergella is dominant throughout this interval. *Heterohelix*, *Guembelitria* and *Globigerinelloides* are also represented. None of the more customary Tethyan genera (*Ticinella* Reichel and *Planomalina* Loeblich & Tappan) are present, and the British faunas cannot be equated with some of the other European successions. Bandy (1967) also recognized the paucity of planktonic species at this level when he described the Lower Cretaceous (Neocomian – Albian) as characterized by a primitive, planktonic fauna. Present research does not extend below the Gault Clay, and it is impossible to place the lower boundary of this zone.

Hedbergella delrioensis – common at most levels
H. infracretacea – common at most levels
H. planispira – common at most levels
H. washitensis – rare, only seen at the Middle/Upper Albian boundary
Heterohelix moremani – common at most levels in the Upper Albian
Guembelitria harrisi – common at most levels in the Upper Albian
Globigerinelloides bentonensis – generally rare, although some concentrations are found, particularly in the Upper Albian

(ii) *Rotalipora evoluta/Praeglobotruncana delrioensis* Zone – Lower & Middle Cenomanian.

Type section: Shakespeare Cliff Borehole, Dover, 1958 (403′1″ to 270′0″) (122·86–82·29 m).

The base of this zone is marked by the appearance of keeled, planktonic foraminifera, and is a readily recognizable horizon. As *R. evoluta* is generally rare, *P. delrioensis* is the more usual indicator encountered in the British successions, although even this species is uncommon (less than 5 % of the total 60/30 grain size fraction) at this level. The *Hedbergella* lineage is still dominant

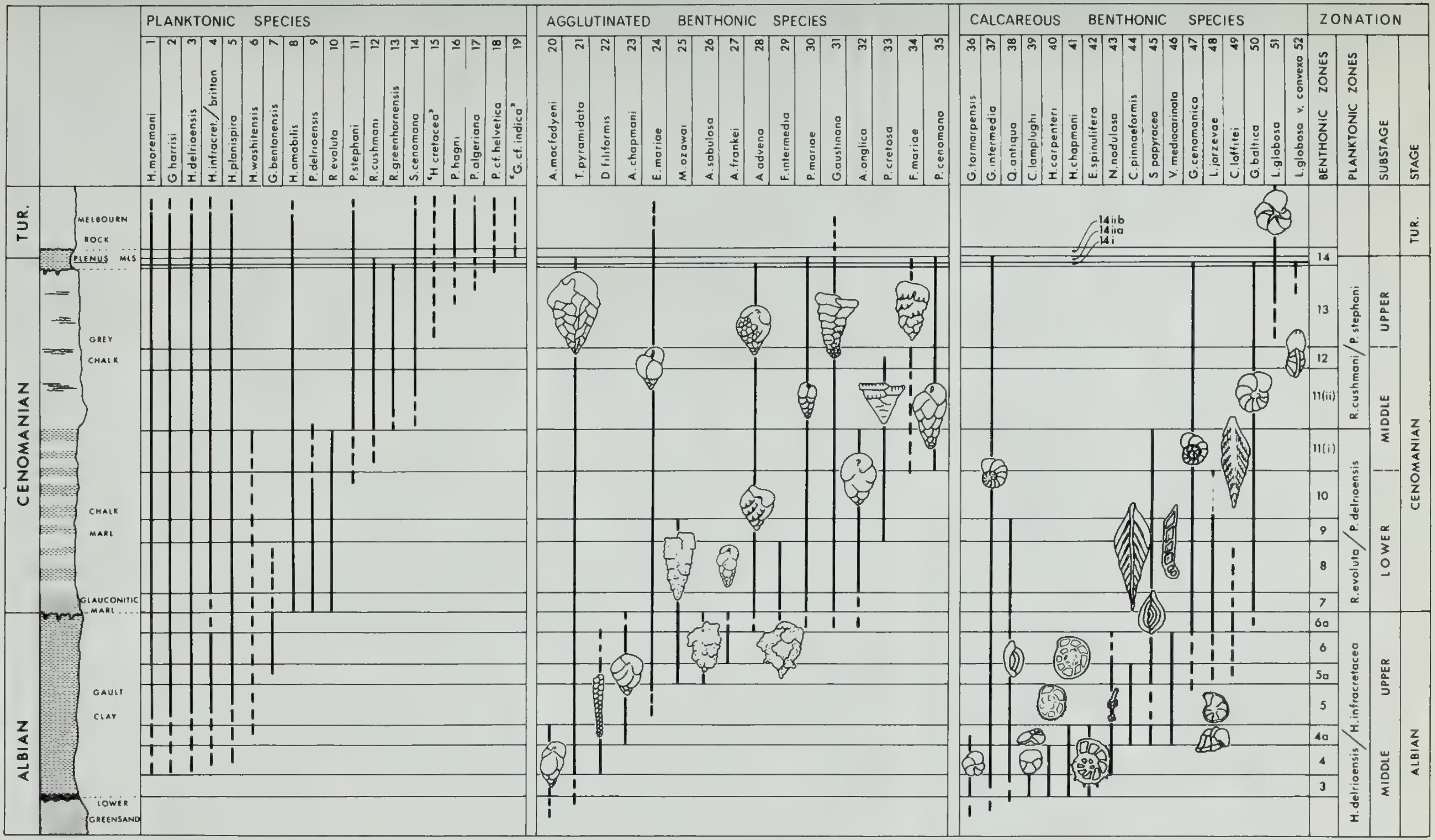


Fig. 9 Fóraminiferal zonation of the mid-Cretaceous (M. Albian – L. Turonian).

numerically. *H. amabilis* has appeared at the base of the zone and *H. brittonensis* replaces *H. infracretacea*. In the upper levels of the zone species more characteristic of the overlying one (iii) begin to appear, although only in small numbers. The early transitional forms between *P. delrioensis* and *P. stephani* are the most conspicuous although primitive forms of *Rotalipora cushmani* have also been recorded. The uppermost few metres of this zone are characterized by the occurrence of *Hedbergella washitensis* in much larger numbers than at any previous level.

Hedbergella amabilis – occurs throughout the zone in small numbers
H. brittonensis – occurs throughout the zone in small numbers
H. delrioensis – common throughout the zone
H. planispira – common throughout the zone
H. washitensis – rare, except in the top few metres of the zone, and at a few scattered horizons at its base
Praeglobotruncana delrioensis – occurs throughout the zone in small numbers
P. stephani – rare, early forms only appear late in the zone
Rotalipora evoluta – rare throughout the zone
R. cushmani – extremely rare, only found late in the zone
Globigerinelloides bentonensis – very rare, but occurs throughout the zone
Heterohelix moremani – common throughout the zone
Guembelitria harrisi – common throughout the zone

(iii) *Rotalipora cushmani/Praeglobotruncana stephani* Zone – Middle & Upper Cenomanian.

Type section: Shakespeare Cliff Borehole, Dover, 1958 (270′0″ to 143′0″) (82·29–43·58 m).

This zone is characterized by the occurrence of very distinctive (*Rotalipora cushmani* and *Praeglobotruncana stephani*) species of planktonic foraminifera, usually in abundance. The total planktonic population in the 60/30 grain size fraction has been found, at certain levels, to exceed 60% of the total, of which a single species (*R. cushmani*) comprises 40%. This general abundance of the planktonic fauna is almost as indicative of the Upper Cenomanian as the species themselves. *R. greenhornensis* is also found throughout this zone although it disappears just before *R. cushmani*. In the upper levels more complex members of the *Praeglobotruncana* group appear, including *P. algeriana*, *P.* cf. *helvetica* and *P. hagni*. These show twin keels unlike the typically Cenomanian species. However, they are very rare and only become abundant in the lower levels of the overlying zone.

Hedbergella amabilis – common throughout the zone
H. brittonensis – common throughout the zone
'*H. cretacea*' – very rare, only seen late in the zone
H. delrioensis – abundant throughout the zone
H. planispira – common throughout the zone
Praeglobotruncana algeriana – very rare, only seen late in the zone
P. delrioensis – seen throughout the zone in small numbers
P. hagni – very rare, only seen late in the zone
P. cf. *helvetica* – very rare specimens found very high in the zone
P. stephani – abundant throughout the zone
Rotalipora cushmani – abundant throughout the zone
R. greenhornensis – seen throughout the zone, although rarely common
Schackoina cenomana – uncommon, but occurring throughout the zone
Globigerinelloides bentonensis – uncommon throughout the zone
Guembelitria harrisi – abundant throughout the zone
Heterohelix moremani – abundant throughout the zone

(iv) *Praeglobotruncana* spp. Zone – Lower Turonian.

Type section: Shakespeare Cliff Borehole, Dover, 1958 (base of zone at 143′0″) (43·58 m).

This zone is defined only in as far as its appearance automatically sets the upper limit of the Cenomanian. A full discussion of the Turonian foraminifera is available elsewhere (Owen 1970), and only passing reference will be made to the species which characterize these levels. The boundary between this zone and the preceding one is the most distinctive in the Cretaceous system, and falls at the base of Jefferies' (1962, 1963) Plenus Marls Bed 4. The *Rotalipora* fauna gives way to a typically twin-keeled *Praeglobotruncana* and *Globotruncana* fauna, and close below this level (base of Jefferies' Plenus Marls Bed 2) there are sweeping changes in the benthonic population. *P. algeriana* and *P. hagni*, while appearing in the Upper Cenomanian, only become common in this zone, and in abundance are diagnostic of it. The zone has not been fully investigated and only a list of the species encountered will be given.

Hedbergella amabilis, *H. brittonensis*, '*H. cretacea*', *H. delrioensis*, *H. planispira*, *Schackoina cenomana*, *Guembelitria harrisi*, *Heterohelix moremani*, '*Globotruncana* cf. *indica*', *Praeglobotruncana algeriana*, *P. hagni*, *P.* cf. *helvetica*, *P. stephani*.

b. Benthonic zonal scheme

Although a wide range of species is used, they belong mainly to three groups. The most important belong in the *Arenobulimina – Flourensina* lineage (Fig. 3, p. 11), which has already been discussed in detail. The *Gavelinella* and *Lingulogavelinella* lineages (Fig. 8, p. 47), while of less diagnostic value, are very useful. The full zonation, with all the planktonic and benthonic species, is shown in Fig. 9, p. 53. This diagram, with the comments in the taxonomic section, makes detailed description unnecessary. Comments of a very general nature are added below.

ZONE 3: Middle Albian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 544′0″ to 524′6″ (165·81–159·87 m). Concurrent Range Zone: *Conorboides lamplughi/Epistomina spinulifera*.

The fauna of this zone is rather limited, although the species are all very distinctive. *C. lamplughi* is not found above it, but *Gavelinella tormarpensis*, *Hoeglundina chapmani*, *H. carpenteri*, *E. spinulifera*, and *Arenobulimina macfadyeni* persist to higher levels.

ZONE 4: Middle Albian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 524′0″ to 487′3″ (159·72–148·51 m). Concurrent Range Zone: *Hoeglundina carpenteri/Dorothia filiformis*.

This zone contains large, highly ornamented specimens of *Epistomina spinulifera*, often in flood abundance, associated with *H. carpenteri*, *H. chapmani* and *D. filiformis*, which continues above.

ZONE 4a: Middle to Upper Albian (transitional). Type section: Dover, No. 1 (Aycliff) (TR 294395) – 487′3″ to 475′0″ (148·51–144·78 m). Concurrent Range Zone: *Epistomina spinulifera/Citharinella pinnaeformis*.

The stratigraphic position of this very thin zone will not be known until investigation of the ammonite fauna has been completed. It contains the typically Upper Albian *Arenobulimina chapmani*, *Nodobacularia nodulosa*, *C. pinnaeformis* and *Spiroloculina papyracea* in association with poorly developed and rather rare specimens of *E. spinulifera*. The zone is not always present, its fauna is rather uneven, and it is possible that the specimens of *E. spinulifera* may be derived.

ZONE 5: Upper Albian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 475′0″ to 416′0″ (144·78–126·80 m). Assemblage Zone: *Citharinella pinnaeformis*.

Arenobulimina chapmani is the dominant species throughout this zone. *C. pinnaeformis* is also present but specimens are fragmentary and never abundant. Other typical species include *Tritaxia pyramidata*, *Nodobacularia nodulosa*, *Dorothia filiformis*, *Spiroloculina papyracea*, *Quinqueloculina antiqua* and the first, rather rare *Eggerellina mariae*.

ZONE 5a: Upper Albian. Type section: Channel Tunnel Site Investigation (1964–65) Borehole No. R.005 – 292′6″ to 289′0″ (89·15–88·09 m). Concurrent Range Zone: *Citharinella pinnaeformis/Arenobulimina sabulosa*.

The appearance of the quadriserial, highly rugose *A. sabulosa*, and *Marssonella ozawai*, in association with *C. pinnaeformis* (which becomes rare at the top of its range) typifies this zone. Other important species are *Tritaxia pyramidata*, *Arenobulimina chapmani*, and *Gavelinella intermedia*. This zone is always very thin, and is often missing.

ZONE 6: Upper Albian. Type section: Dover, No. 1, (Aycliff) (TR 294395) – 414′0″ to 403′1″ (126·19–122·86 m). Concurrent Range Zone: *Vagulina mediocarinata/Arenobulimina frankei.*

Where Zone 6a is missing *A. frankei* is restricted to this zone. *A. sabulosa* and *A. chapmani* are the dominant species, usually associated with *Marssonella ozawai* and *Tritaxia pyramidata. V. mediocarinata* does not persist above this zone. *Dorothia filiformis* and *Nodobacularia nodulosa* are very rare and not always present.

ZONE 6a: Upper Albian to Lower Cenomanian (transitional). Type section: Channel Tunnel Site Investigation (1964–65) Borehole No. R.005 – 289′0″ to 246′6″ (88·09–80·62 m). Concurrent Range Zone: *Arenobulimina sabulosa/Flourensina intermedia.*

This zone, with its distinctive fauna containing large specimens of *Citharinella laffittei*, yields both Upper Albian and Cenomanian benthonic species in addition to transitional forms. Typically Albian species: *A. chapmani, A. sabulosa, A. frankei*, etc. (in lower part of zone). Typically Cenomanian species: *A. advena, F. intermedia, Gaudryina austinana, Gavelinella cenomanica*, etc. (in the upper part of the zone). Intermediate forms: *A. chapmani/A. advena, A. sabulosa/A. anglica, G. intermedia/G. cenomanica*, and *A. frankei/Plectina mariae*. Although planktonic species are associated with the benthonic population no keeled forms have ever been found. The latter first appear in Zone 7, suggesting that Zone 6a is late Upper Albian in age.

Zone 6a has a peculiar geographical distribution. It has been found only in boreholes in the north-western part of the English Channel between Dover and Cap Blanc Nez, in the Upper Greensand exposures in Surrey between Godstone and Betchworth, and possibly in the Fetcham Mill Borehole. Elsewhere it is cut out by the Albian/Cenomanian non-sequence. In the Channel it occurs as a small sedimentary cycle, rich in white mica and sharply truncated by the overlying 'Glauconitic Marl'. The base of the cycle is lithologically almost indistinguishable from the latter, but where the cycle is thick (i.e. off Dover) the two are separated by micaceous marls rich in disseminated glauconite.

No ammonites have been found in Zone 6a, but its probably very late Upper Albian age and restricted distribution suggest that it may be equivalent to the whole or a part of the *Stoliczkaia dispar* Zone.

ZONE 7: Lower Cenomanian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 403′1″ to 401′9″ (122·86–122·45 m). Concurrent Range Zone: *Plectina mariae/Bulbophragmium aequale folkestoniensis* (Chapman).

This zone contains the first, purely Cenomanian benthonic fauna, dominated by *Arenobulimina advena, Flourensina intermedia, Marssonella ozawai, Plectina mariae, Gavelinella baltica, Lingulogavelinella jarzevae*, and very large, coarsely agglutinated Lituolacea (i.e. *B. aequale folkestoniensis* (Chapman)). This zone coincides with the 'Glauconitic Marl' and the abundance of the large Lituolacea is facies-controlled. In the absence of the typical lithology Zones 7 and 8 are not easily separated.

ZONE 8: Lower Cenomanian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 401′9″ to 362′10″ (122·45–110·59 m). Concurrent Range Zone: *Flourensina intermedia/Arenobulimina anglica.*

F. intermedia in association with abundant *A. anglica* characterize this zone. *A. advena, Marssonella ozawai, Tritaxia pyramidata* and other agglutinated species continue up from below but *B. aequale folkestoniensis* is replaced by the less coarsely agglutinated *B. aequale aequale* (Reuss). Other common species include *Eggerellina mariae, Plectina mariae, Spiroloculina papyracea, Gavelinella intermedia, G. cenomanica* and *G. baltica.*

ZONE 9: Lower Cenomanian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 362′10″ to 337′0″ (110·59–102·72 m). Concurrent Range Zone: *Marssonella ozawai/Pseudotextulariella cretosa.*

In Zone 9 *M. ozawai* and *Lingulogavelinella jarzevae* are found in association with *P. cretosa.*

Flourensina intermedia is absent, but *Tritaxia pyramidata*, *Eggerellina mariae*, *Arenobulimina advena*, *A. anglica*, *Gavelinella intermedia*, *G. cenomanica* and *G. baltica* continue up from below.

Zone 10: Lower Cenomanian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 337′0″ to 290′0″ (102·72–88·39 m). Assemblage Zone: *Pseudotextulariella cretosa*.

Zone 10 yields *Tritaxia pyramidata*, *Eggerellina mariae*, *Arenobulimina advena*, *Plectina mariae*, *Gaudryina austinana*, *Pseudotextulariella cretosa*, *Gavelinella intermedia*, *G. cenomanica* and *G. baltica*, but no *Marssonella ozawai* or *P. cenomana*. *Lingulogavelinella jarzevae* reappears in a thin band near its top in south-east England.

Zone 11(i): Middle Cenomanian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 290′0″ to 270′0″ (88·39–82·30 m). Concurrent Range Zone: *Arenobulimina anglica*/*Plectina cenomana*.

The beginning of the Middle Cenomanian is characterized by the appearance of *P. cenomana*, although the remainder of the fauna remains unchanged. In this zone this species is in association with *Spiroloculina papyracea* and *A. anglica*.

Zone 11(ii): Middle Cenomanian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 270′0″ to 225′0″ (82·30–68·58 m). Assemblage Zone: *Plectina cenomana*.

This zone is differentiated from Zone 11(i) primarily on planktonic foraminifera. Its base is the mid-Cenomanian non-sequence, and with the onset of deeper water conditions *Arenobulimina anglica* and *Spiroloculina papyracea* disappear. The upper limit of the zone nearly coincides with the disappearance of *Pseudotextulariella cretosa*, which finally dies out just above the base of the very thin Zone 12.

Zone 12: Middle Cenomanian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 225′0″ to 220′0″ (68·58–67·06 m). Acme Zone: *F. mariae*.

Zone 12 is characterized by the appearance of large and abundant specimens of the very distinctive *Flourensina mariae* (total range from Zone 11(ii)–14(i)). *Pseudotextulariella cretosa* dies out just above its base and there is evidence of a return to shallow water conditions at this level. The fauna is sometimes abraded and in some sections this zone is terminated above by a weakly developed non-sequence.

Zone 13: Upper Cenomanian. Type section: Dover, No. 1 (Aycliff) (TR 294395) – 220′0″ to 147′0″ (67·06–44·81 m). Assemblage Zone: *Lingulogavelinella globosa*.

Zone 13 yields an association of *Tritaxia pyramidata*, *Eggerellina mariae*, *Arenobulimina advena*, *Plectina mariae*, *Gaudryina austinana*, *Flourensina mariae*, *P. cenomana*, *Gavelinella intermedia*, *G. baltica* and *G. cenomanica*, with *L. globosa* which is not found below.

Zone 14: Upper Cenomanian/Lower Turonian. This zone coincides with the *Actinocamax plenus* marls of Jefferies (1962, 1963). We are in agreement with many of the conclusions of Jefferies, and only disagree with the overall placing of the marls in the Turonian Stage. The decision to place the Cenomanian/Turonian boundary within this marl unit will be discussed in detail in a later section. The division of the Plenus Marls into eight lithologically and faunally distinctive beds has been corroborated. The recognition of an important erosion surface below the Plenus Marls, as well as at four levels within the sequence, agrees with the present research although we would attach more importance to the pre-Bed 4 erosion surface and less to the sub-Plenus Marls erosion surface.

Zone 14 can be split into two distinct units (14(i) and 14(ii)) on the basis of the marked faunal change at the base of Bed 2. (See Fig. 9, p. 53.)

Zone 14(i): Upper Cenomanian. Type section: Merstham Greystone Limeworks (TQ 295542). Bed 1 of Jefferies (1962, 1963). Acme Zone: *Lingulogavelinella globosa* var. *convexa*.

This zone contains the same typically Cenomanian species as Zone 13 accompanied by very abundant *L. globosa* var. *convexa* and *Arenobulimina depressa* (Perner) (see Fig. 3, p. 11).

ZONE 14(ii): Upper Cenomanian and Lower Turonian. Type section: Merstham Greystone Limeworks (TQ 295542). Base of Zone at base of Bed 2 of Jefferies (1962, 1963). Assemblage Zone: *Arenobulimina preslii* (Reuss).

Zone 14(ii) contains none of the typically Cenomanian species and the benthonic fauna as a whole becomes less diverse. Assemblages rich in internally subdivided members of the genus *Arenobulimina* are replaced by those containing the internally simple *A. depressa*, *A. truncata* (Reuss) and *A. preslii* (see Fig. 3). *Eggerellina mariae*, *Gaudryina austinana* and *Lingulogavelinella globosa* persist up from below, and often form appreciable proportions of the assemblage.

c. Combined planktonic and benthonic zonal scheme; subdivision of Zone 14

Whereas the zonation based on planktonic foraminifera provides a firm basis for long-range correlation and the delimitation of stage boundaries it is too coarse for the solution of many correlation problems. The benthonic zonation is much finer, but some of the subdivisions are poorly defined and admittedly unsatisfactory. The use of both in conjunction makes the zonal boundaries more definitive where coincident and permits additional subdivision where they are not. In particular Zone 14(ii) can be subdivided further.

ZONE 14(iia): Upper Cenomanian. Type section: Merstham Greystone Limeworks (TQ 295542). Beds 2 and 3 of Jefferies (1962, 1963). Assemblage Zone: *Arenobulimina preslii/Rotalipora cushmani.*

This zone is characterized by the association of Cenomanian planktonic species (*R. cushmani*, etc.) with a benthonic association more typical of the Turonian (*A. depressa*, *A. truncata*, *A. preslii*, *Eggerellina mariae*, *Tritaxia tricarinata* (Reuss), *Gaudryina austinana*, *Lingulogavelinella globosa*, etc.).

ZONE 14(iib): Lower Turonian. Type section: Merstham Greystone Limeworks (TQ 295542). Base of zone at base of Bed 4 (Jefferies 1962, 1963). Assemblage Zone: *Arenobulimina preslii/ Praeglobotruncana hagni.*

Zone 14(iib) contains the same benthonic association as Zone 14(iia) with abundant Turonian planktonic species ('*Globotruncana* cf. *indica*', *P. hagni*, *P. algeriana*, etc.).

Although the subdivisions of Zone 14 proposed here are easily recognizable, we consider their use inadvisable in the arguments set out herein. The position of the Cenomanian/Turonian boundary and the Cenomanian stratigraphy of south-west England is more easily clarified using the synchronous but more finely drawn Plenus Marls Bed number sequence of Jefferies (1962, 1963).

Determination of stage boundaries

Following the standard practice of defining only the base of a stage, two such levels are discussed.

a. Base of the Cenomanian Stage

The type area for the Cenomanian, according to d'Orbigny (1847, 1850), is the area of Sarthe in western France. Here the majority of workers have drawn the base of the stage at the base of the 'argille glauconieuse à minerai de fer' (Guillier 1886, Delaunay 1934, Sornay 1957, Hancock 1959 and Juignet 1968). Hancock (1959) regards this horizon as the base of the 'zone à *Mantelliceras mantelli*'. Kennedy (1969) divided the Lower Cenomanian (Zone of *M. mantelli*) into the three assemblage subzones, of *Hypoturrilites carcitanensis*, *Mantelliceras saxbii* and *M. dixoni.* The appearance of the *H. carcitanensis* assemblage fauna would therefore mark the base of the Cenomanian in the British successions.

The Lower Cenomanian sands in the Sarthe are decalcified and direct microfaunal studies have unfortunately been attempted only recently. No results are available, and indeed the chance of a large fauna being found is very slight.

In the south-east of England Kennedy (1969) records the occurrence of the *H. carcitanensis* assemblage in several localities. While this horizon is poor in the Folkestone/Dover section, Kennedy (1969 : 474) notes 'ammonites, probably of *H. carcitanensis* assemblage, range up to 2r, but completely diagnostic forms are absent. 2v has yielded what seems to be a *Mantelliceras saxbii* assemblage ammonite'. While the weakness of the evidence for a *H. carcitanensis* assemblage undoubtedly troubled Kennedy he still (1969 : fig. 16) correlated it with the excellent *H. carcitanensis* assemblage from Beddingham, Sussex.

As the microfaunal control is more satisfactory at Dover and Folkestone the base of the Glauconitic Marl at East Wear Bay has been taken as the base of the Cenomanian. The main elements of the microfauna taken as being indicative of this level are the appearance of the *Rotalipora evoluta/Praeglobotruncana delrioensis* Zone fauna, and the appearance of large numbers of *Arenobulimina advena* (replacing *A. chapmani*) and *Flourensina intermedia* (replacing *A. sabulosa*) as the dominant elements of the fauna. The most important feature of this faunal turnover is the appearance of the keeled planktonic foraminifera. The majority of recent workers – Pessagno (1967), Bandy (1967) and Douglas (1969a, b) – consider the appearance of the *Rotalipora* fauna as indicative of this level. The base of the Cenomanian in Great Britain is therefore taken as the base of the Glauconitic Marl in East Wear Bay (Folkestone), and can be recognized faunally as the base of the *R. evoluta/P. delrioensis* Zone (base of Zone 7 on the benthonic scheme).

b. Base of the Turonian Stage

Unlike the Cenomanian, this boundary has been the source of much confusion. The suggestions of Bandy (1967) and Pessagno (1967) have been largely ignored as they were not based on the type area, and lacked macrofaunal control. Work is still in progress on the fauna of the basal Turonian of the type area, and only an outline of the problem and some preliminary results can be given here.

One of the most recent works on the Turonian is that of Butt (1966), who proposed a complete succession of lithostratigraphic units based on the Cher Valley. This largely followed the work of Lecointre (1959) even though he was at some variance with many other workers in this field. It is necessary therefore to trace events from the initial definition of the stage, and the following is a short summary of the relevant work on the type sections of the Touraine (and the Sarthe).

In 1842 d'Orbigny erected the Turonian Stage with the comments

> . . . Je propose de désigner à l'avenir l'étage que m'occupe (craie chloritée, glauconie crayeuse, craie tuffeau, et grès verts) sous le nom de Turonien, de la ville de Tours (Turones) ou de la Touraine (Turonia) situées sur ces terrains.

In 1847 d'Orbigny himself redefined the stage, erecting the Cenomanien Stage to include the lower part of his previously defined Turonien. The section of the Frétevou Chalk (Butt 1966) and the succession in the Cher Valley was known to such workers as de Grossouvre (1889, 1901) and Faupin (1908), but it was Lecointre (1959) who first defined the type section of the Turonian Stage within this area. Immediately prior to this work, however, Sornay (1957) had defined the base of the Turonian as the base of the *Inoceramus labiatus* (or *Mammites nodosoides*) Zone. Lecointre (1959 : 421), while recognizing that this faunal association was 'characteristic' of the 'craie marneuse à chaux hydraulique', included, below this level – and still within the Turonian – the 'marnes à *Terebratella carentonensis*', the 'marnes à *Ditrupa deforme*' and the 'Sables de Bousse'. Unfortunately the text-figure in which this relationship was explained does not really correspond to the text (Lecointre 1959 : 419–420), where he describes the lateral variations in facies recorded at this level. The following is a short abstract from his list of important variations (Fig. 10).

> 1. La craie marneuse sans silex occupe toute la surface de la Touraine *sensu lato* et varie: parfois moins argileuse, plus sèche, parfois au contraire donnant sans mélange de la bonne chaux hydraulique . . .
>
> Par sa base, elle est susceptible de varier considérablement. Les faciès arénacés du Cénomanien peuvent survivre à cette époque et se prolonger dans la base du Turonien, sable à *Catopygus* de Bousse, marnes à *Terebratella carentonensis*, marnes à *Ditrupa deformis* de l'Anjou et du Maine.
>
> Aucune Ammonite n'a été recueillie dans ces niveaux, aussi peut-on soutenir qu'elles appartiennent au Cénomanien (de Grossouvre 1901, p. 766).

It seems that these distinctive facies of the basal Turonian were regarded by Lecointre as local variations in the area immediately adjacent to the type sections. Butt (1966) only studied a single section in the Cher Valley and did not even mention the stratigraphic position of these local variations. His description of the foraminifera of the Frétevou Chalk ('craie marneuse sans silex') does however eliminate many of the problems facing micropalaeontologists. *Rotalipora* spp. was

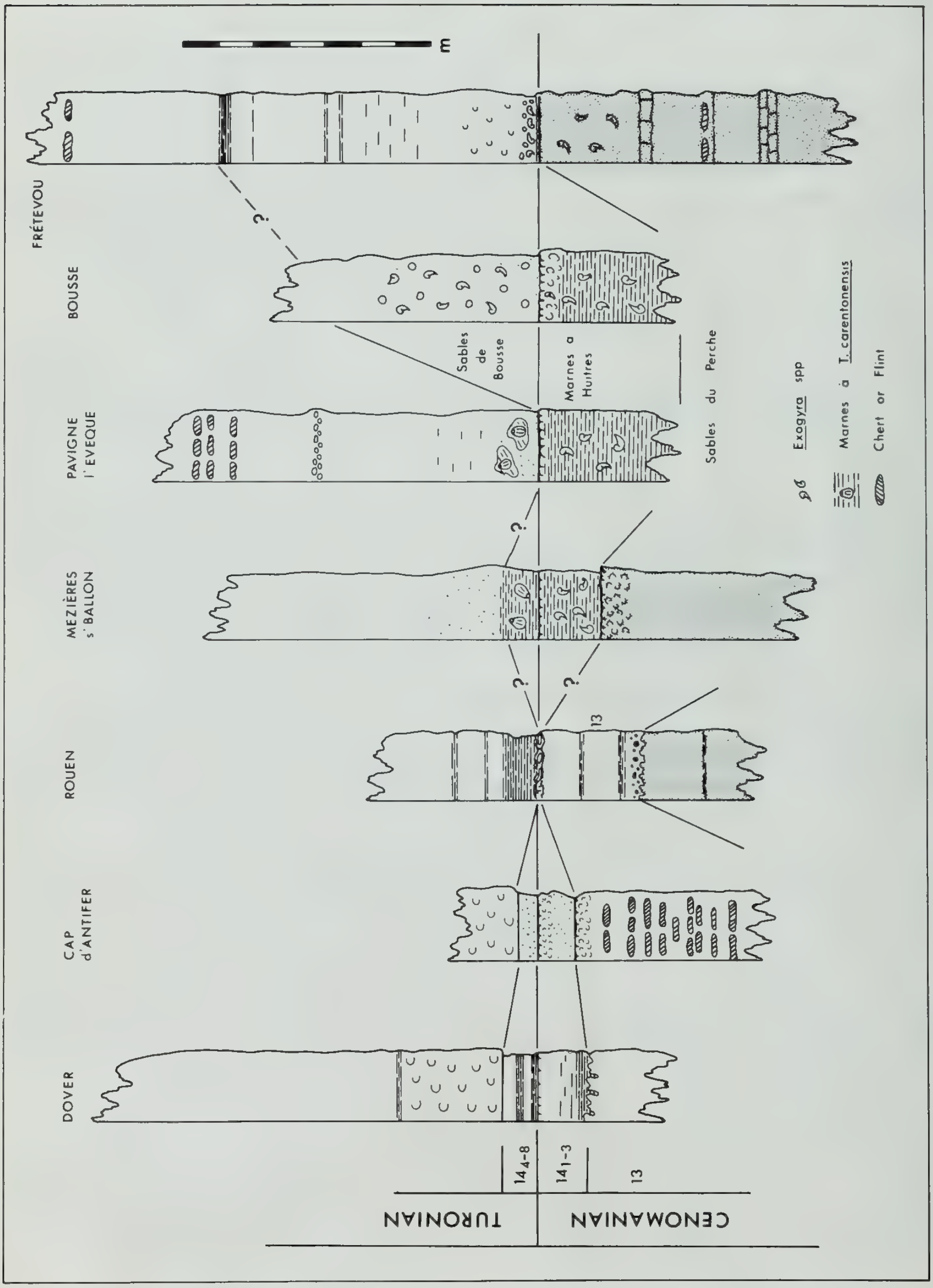

DOVER
CAP d'ANTIFER
ROUEN
MEZIÈRES s' BALLON
PAVIGNE l'EVEQUE
BOUSSE
FRÉTEVOU
TURONIAN
CENOMANIAN
14₄-8
14₁-3
13
13
m
Sables de Bousse
Marnes a Huitres
Sables du Perche
Exogyra spp
Marnes à T. carentonensis
Chert or Flint

Fig. 10 The Cenomanian/Turonian boundary in southern England and northern France. The nodular chalk near the base of the Turonian in the Dover succession is the local equivalent of the Melbourn Rock.

not recorded by Butt from the Frétevou Chalk nor has it been found by us in any previously described 'Turonian' chalk, from either the type area or southern England. This confirms Marks' (1967) contention that the *Rotalipora* fauna is characteristically Cenomanian and the Turonian age of beds from which *R. cushmani* (or *R. turonica*) has been recorded is suspect. Marks (1967: table 3) indicated the previously recorded ranges of *R. cushmani*. The appearance of this species in the mid-Cenomanian as recorded by Marks, and its continuation to the Cenomanian/Turonian boundary as recorded by Malapris & Rat (1961a, b), is in agreement with the British successions.

The planktonic foraminifera recovered from the Frétevou Chalk by Butt (1966) and ourselves include *Praeglobotruncana stephani*, *P. hagni* and *Hedbergella delrioensis*. This association, together with abundant *Lingulogavelinella globosa*, has only been recorded from:

1. the 'marnes à *Terebratella carentonensis*',
2. the 'Sables de Bousse',
3. the Plenus Marls (Beds 4–8) and
4. the *Praeglobotruncana roddai* (? = *P. hagni*) Subzone of northern California as described by Douglas (1969b), which occupies a thickness of several hundred feet.

The correlation scheme shown in Fig. 9 (p. 53) summarizes the present state of microfaunal knowledge of this succession, and although work is not complete a pattern is beginning to emerge. The main feature is the reported first appearance of *Inoceramus labiatus* at a horizon above the Plenus Marls (W. J. Kennedy, *pers. comm.*). This agrees with Lecointre's (1959) observation that *I. labiatus* appears above the base of the 'craie marneuse sans silex' in the type section. Describing the Frétevou Chalk succession, Lecointre includes a bed of 'craie marneuse grise à *Rhynchonella cuvieri* d'Orbigny' between the beds of 'craie marneuse blanche micacée à nombreux *Inoceramus labiatus* Brongniart' and the underlying oyster-bearing Cenomanian glauconitic sands. The thickness of this *I. labiatus*-free chalk is not given and the field work of one of us (M. B. H.) on this section gave no reliable figure. While *I. labiatus* may characterize the Lower Turonian, it is not the best species with which to define the base of the Turonian in the type section.

The planktonic microfauna of the basal Frétevou Chalk includes:

Praeglobotruncana algeriana – uncommon
P. hagni – very common
P. stephani – abundant
Hedbergella delrioensis – abundant

The *Rotalipora* fauna is not present and one only can deduce that this genus is not represented in the Turonian. As the above-listed fauna is also recorded from the 'marnes à *T. carentonensis*' and the 'Sables de Bousse', Lecointre was correct in suggesting that these locally-developed facies are lateral equivalents of the basal Turonian. The rather poor benthonic fauna of the Frétevou Chalk corresponds very well with that recorded from the Plenus Marls (Beds 4–8). The base of the Turonian is therefore drawn at the erosion surface between Beds 3 and 4 of the Plenus Marls sequence. This restricts the *Rotalipora* fauna to the Cenomanian, as suggested by Bandy (1967), Pessagno (1967), Marks (1967) and Douglas (1969b). The change from the *Praeglobotruncana*/*Rotalipora* fauna of the Cenomanian to the *Praeglobotruncana*/*Globotruncana* fauna of the Turonian can be recognized all over the world and it is suggested that the base of the Plenus Marls Bed 4 is the most acceptable level for such an important boundary.

The mid-Cenomanian non-sequence

The placing of the Cenomanian/Turonian boundary where stated above permits accurate correlation of the British successions with those overseas. The section provided by Eicher (1969b) from the western interior of the United States is one of the most suitable for detailed comparison (Fig. 11). The most interesting feature is the sudden change from a predominantly benthonic population to a largely planktonic one within the mid-Cenomanian. Although the actual percentage change is not so large in southern England, it is nevertheless of the same order and must indicate some fundamental change in the depositional pattern in both areas. As this population change is of considerable importance it will be discussed in detail.

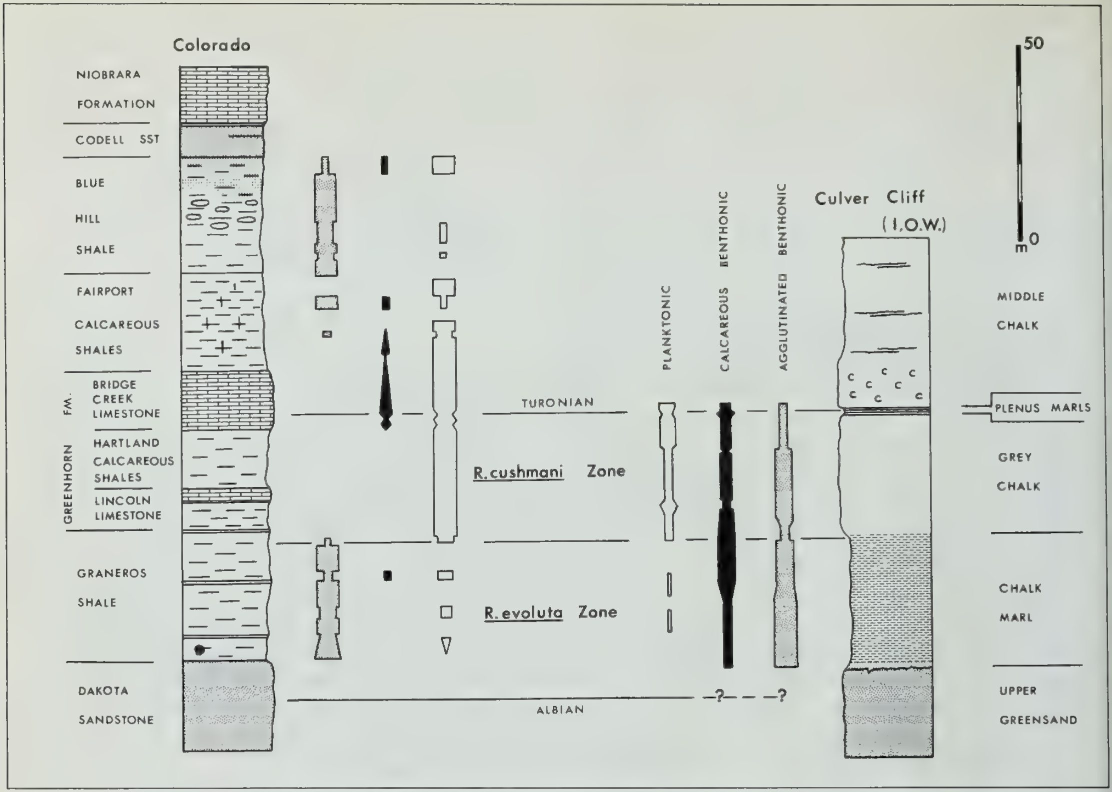

Colorado
NIOBRARA FORMATION
CODELL SST
BLUE HILL SHALE
FAIRPORT CALCAREOUS SHALES
GREENHORN FM.
BRIDGE CREEK LIMESTONE
HARTLAND CALCAREOUS SHALES
LINCOLN LIMESTONE
GRANEROS SHALE
DAKOTA SANDSTONE
TURONIAN
R. cushmani Zone
R. evoluta Zone
ALBIAN
?
?
PLANKTONIC
CALCAREOUS BENTHONIC
AGGLUTINATED BENTHONIC
Culver Cliff (I.O.W.)
50
0
m
MIDDLE CHALK
c
PLENUS MARLS
GREY CHALK
CHALK MARL
UPPER GREENSAND

Fig. 11 Microfaunal comparison of the successions in Colorado and the Isle of Wight (England).

Grimsdale & van Morkhoven (1955) attempted to formulate a method facilitating accurate estimation of the depth of deposition from analysis of faunal contents of samples. It had long been appreciated that a thanatocoenosis in an abyssal sediment from above the compensation depth would contain 90–100% planktonic foraminifera, while one from the neritic zone would be almost totally composed of benthonic individuals. However, no practical means of integrating this information into a method for determining the depth of deposition has been developed. Grimsdale & van Morkhoven's attempts used the faunal counts of samples collected on twelve traverses (largely neritic) made by Phleger & Parker (1951). Grimsdale & van Morkhoven discussed the lack of correspondence of their graphs and, after compiling a list of the limitations, concluded that while the theory was basically sound the depth of deposition could not be accurately estimated using this technique. More recently Eicher (1969a) has used population percentages to demonstrate, in a general way, the deepening and subsequent shallowing of the Greenhorn Sea in Colorado.

Flexer & Starinsky (1970), however, based the bulk of their work on the assumption of a direct relationship between the planktonic-benthonic ratio and the depth of deposition. This was following Eicher (1969a), and many other workers had concluded that determinations based only on planktonic/benthonic ratios may give incorrect results owing to the variation of such parameters as salinity, light penetration, availability of nutrients and, perhaps more significantly, temperature. We favour Eicher's broad approach and conclude that in the mid-Cenomanian of southern England, as in the United States, there was a *general* deepening of the seaway.

The planktonic/benthonic ratio plot for the Shakespeare Cliff (Dover) borehole (Fig. 12a), based on the 60/30 grain size fraction, shows the variations recorded from the Cenomanian succession at this locality. This graph shows the marked microfaunal change in the mid-Cenomanian

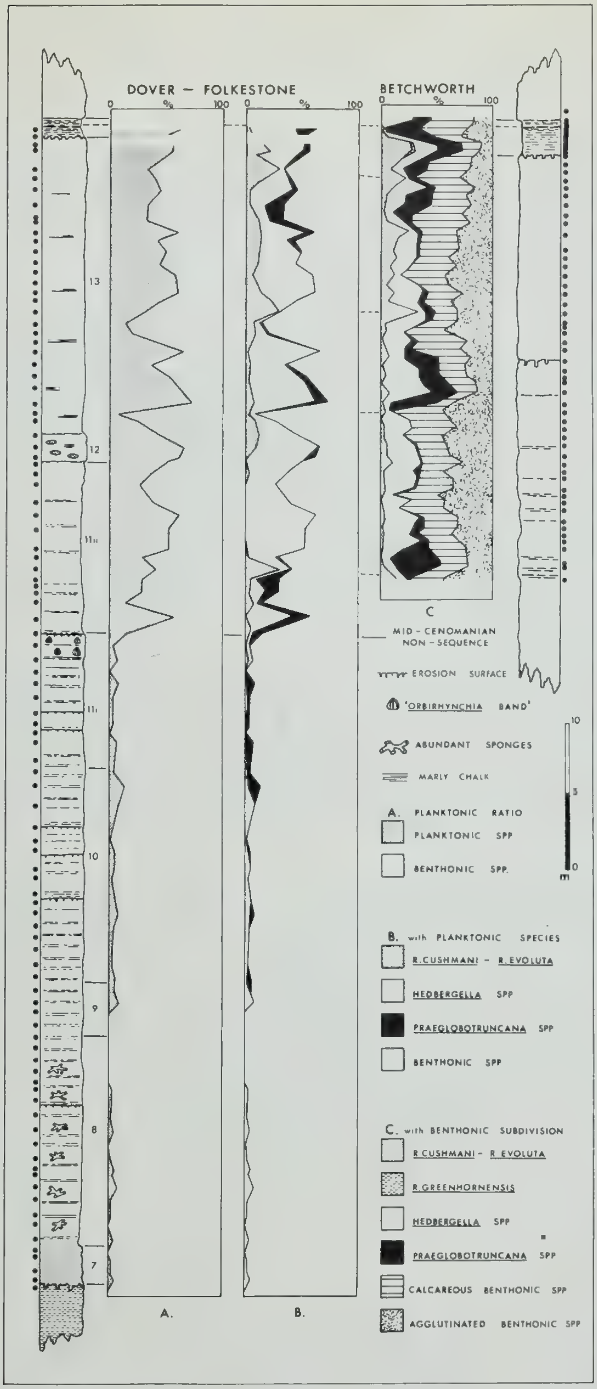


Fig. 12 Planktonic/benthonic ratio graphs, based on counts of the 60/30 grain-size fraction.
a. Outline planktonic/benthonic ratio graph for the Dover borehole.
b. Modified graph, with generic subdivision within the planktonic unit.
c. Complete analysis of the Betchworth section, with some tentative correlations with the Dover succession. (Black dots indicate sample positions.)

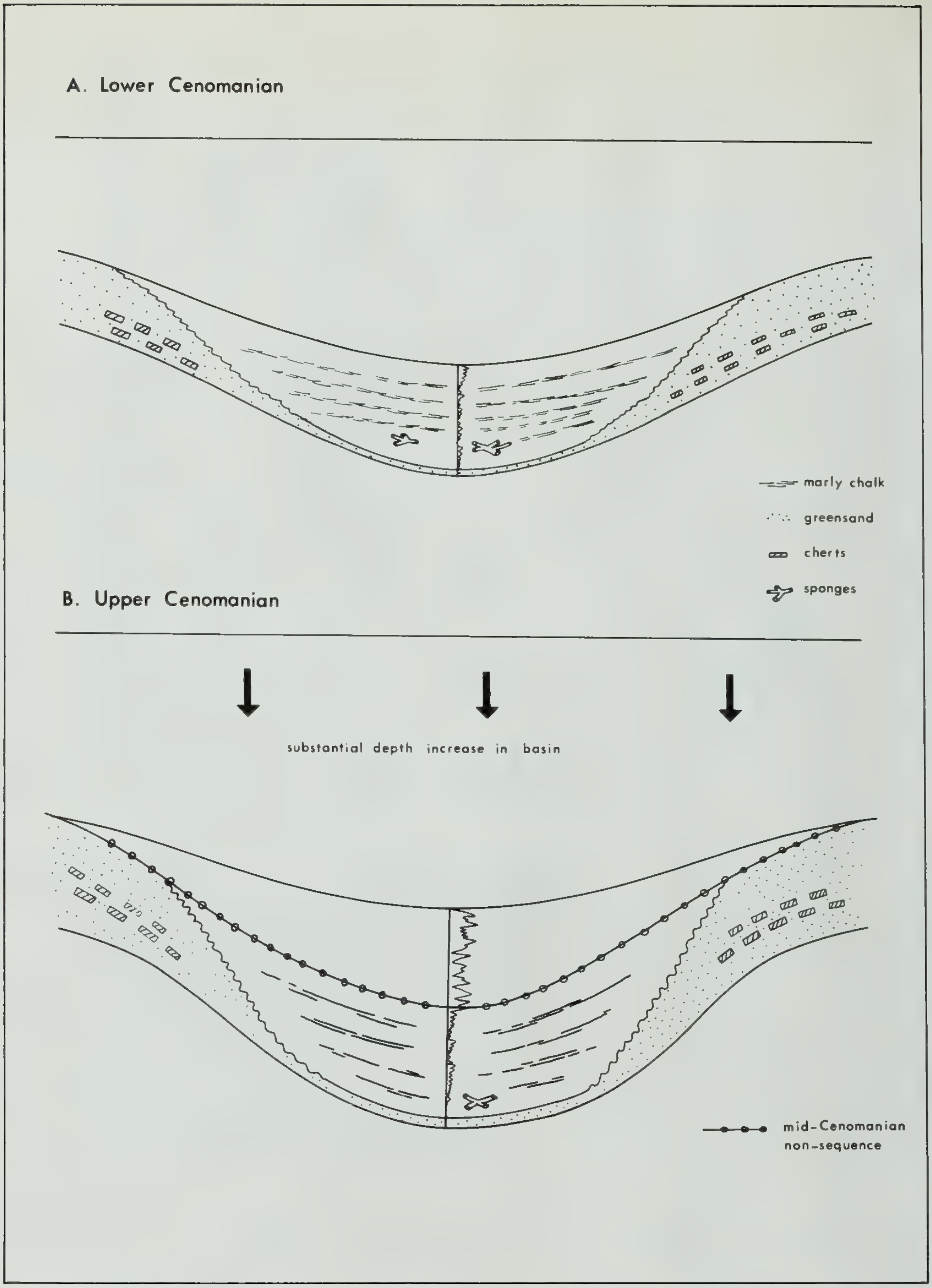

A. Lower Cenomanian
marly chalk
greensand
cherts
sponges
B. Upper Cenomanian
substantial depth increase in basin
mid-Cenomanian non-sequence

Fig. 13 Model showing the development of the planktonic/benthonic ratio graph in the Lower Chalk of south-east England.

and it is suggested that it relates to the development of the Atlantic Ocean. A model (Fig. 13) for this deepening has been developed for the Cenomanian in southern England and this will be used in the following stratigraphic analysis. The principle is that of Grimsdale & van Morkhoven (1955), although we would never attempt to attach accurate depth values to the various values of the planktonic populations.

A single major depth change does not, however, account for the planktonic/benthonic variations recorded above and below the mid-Cenomanian. Explanation of these fluctuations in terms of depth variations would require eustatic oscillations throughout the whole of the Cenomanian. While there are many distinctive sedimentological changes within the Cenomanian chalk there are none related to depth changes consistently corresponding to the planktonic/benthonic ratio changes.

Further investigation of the planktonic distribution throughout the same section shows even more significant variations. The most important single feature arising from the modified graph (Fig. 12b) is the distribution of the *Rotalipora* group, in particular *R. cushmani*. This species appears in large numbers at the mid-Cenomanian non-sequence and above this level is seen to dominate the planktonic fauna of certain horizons. These intervals of relative abundance were short-lived, although they can be traced laterally over much of southern England. One of the most striking comparisons is between the section at Dover and that recorded by Diver (1968) from the Betchworth Limeworks, Surrey (Fig. 12c). These two graphs can be correlated easily, even though the two localities are nearly 100 km apart. The close correspondence of the faunal populations at particular stratigraphic levels must be due to a similarity in the conditions of deposition, and in attempting to elucidate the reasons behind this pattern the following points are relevant.

1. While one can relate the faunal change in the mid-Cenomanian to an increase in the depth of the Cenomanian sea, it seems unlikely that all the changes above and below this level can be attributed to the same cause.
2. The features producing the faunal changes – in particular the levels of abundant *Rotalipora* – appear to be of relatively short duration.
3. Individual features of the graphs can be traced laterally over considerable distances, and therefore a mechanism that can affect hundreds of square miles of sea floor has to be considered.

If water depth was the major controlling influence the total number of planktonic individuals would be expected to diminish towards the margin of the basin. This is not always the case and in west Dorset and south Devon values of nearly 40% have been recorded for the planktonic component of the fauna. This indicates some other distribution control, allowing the planktonic individuals access to these more marginal environments. The levels of abundant *Rotalipora* are therefore thought to be indicative of warmer water conditions, and the oscillations shown in Fig. 11c indicative of the passage of warm water currents over the whole of southern England. Periodically shifting water masses, alternately warmer and cooler, could provide the large areal coverage required to explain the lateral consistency of the graphs. While the depth changes could still occur, this explanation obviates the need for marked eustatic changes at frequent intervals. Their effects, over an area as small as southern England, would be essentially synchronous.

It is suggested that a detailed study of the planktonic/benthonic ratios for the Cenomanian, as well as other stages in the Upper Cretaceous, could shed much light on the problem of chalk deposition. However, the study of chalk deposition, phytoplankton production and their relationship to palaeocurrents is beyond the scope of this paper (Hart & Carter 1975).

The oscillations in the value of the planktonic-benthonic ratios, while occurring in the Lower Cenomanian on a very limited scale, are more prominent above the mid-Cenomanian non-sequence. The level at which this change occurs deserves detailed attention. It displays one of the most striking faunal changes recorded in the whole of the mid-Cretaceous, and its field relationships must be described. It is a non-sequence that can be located at many places in southern England. The most characteristic exposure is that between Folkestone and Dover, at the foot of Acker's Steps. Under the edge of the concrete sea defences the characteristic limestone/marl cycles of the Chalk Marl are visible on the foreshore. These become less marly upwards, and terminate abruptly at a burrowed surface marking a hiatus in deposition. Darker sediment from above fills the burrows and small fragments of material from below are sometimes found resting on the burrowed surface. Four of these cycles contain abundant *Orbirhynchia mantelliana* (J. Sowerby) in a fauna that places these beds in the *Turrilites costatus* Assemblage Zone of Kennedy (1969). At the top of a particularly strong cycle the brachiopod fauna disappears and it is at this level that the microfaunal change occurs. While it is possible to demonstrate an angular discordance between foraminiferal zones at this level on plotted cross-sections, in the field in south-east England it is recognizable only as the top of a particularly well-developed cycle. In Cambridgeshire, Bedfordshire and Buckinghamshire, however, this part of the succession is marked by the appearance of a series of hard limestone beds, each usually underlain by a thin band of slightly rounded pale brown phosphates. This series of limestones is known either as the Totternhoe Stone, the Burwell Rock or the Chilton Stone, depending on the locality. While the phosphate horizon indicates the level of the most important environmental change, it does not mark the non-sequence, which is found a few centimetres further up. However, the non-sequence still corresponds with the top of the *Orbirhynchia mantelliana* band. Jeans (1968) recognized the importance of this brachiopod 'pulse fauna' and related this particular level to those of other 'pulse faunas' found throughout the Lower Chalk. The presence of the phosphate bed below the brachiopod level indicates a period of shallowing prior to the deepening effect of the non-sequence. This shallowing has also been demonstrated by Burnaby (1962) using the benthonic foraminifera of the Chalk Marl succession at Barrington (Cambridgeshire). Although the effect is less well marked in south-east England, a similar temporary decrease in water depth is reflected by the reappearance of rare specimens of *Lingulogavelinella jarzevae* and the occasional occurrence of specimens of

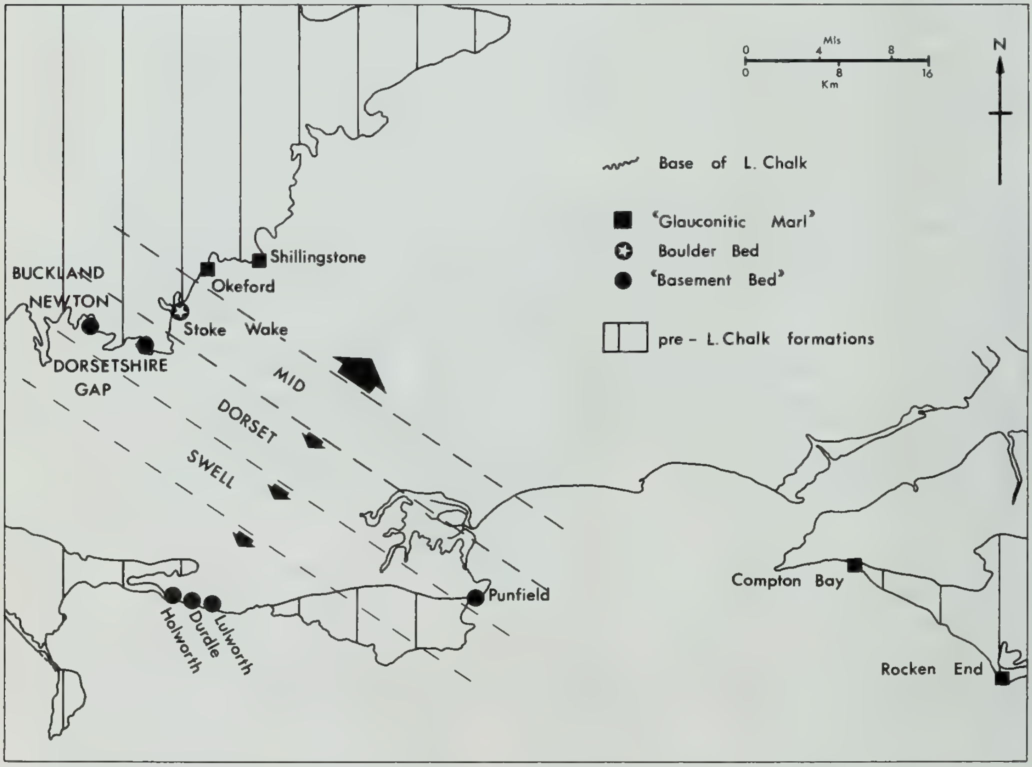


Fig. 14 The variation in the form of the 'Basement Bed' of the Lower Chalk in Hampshire and Dorset.

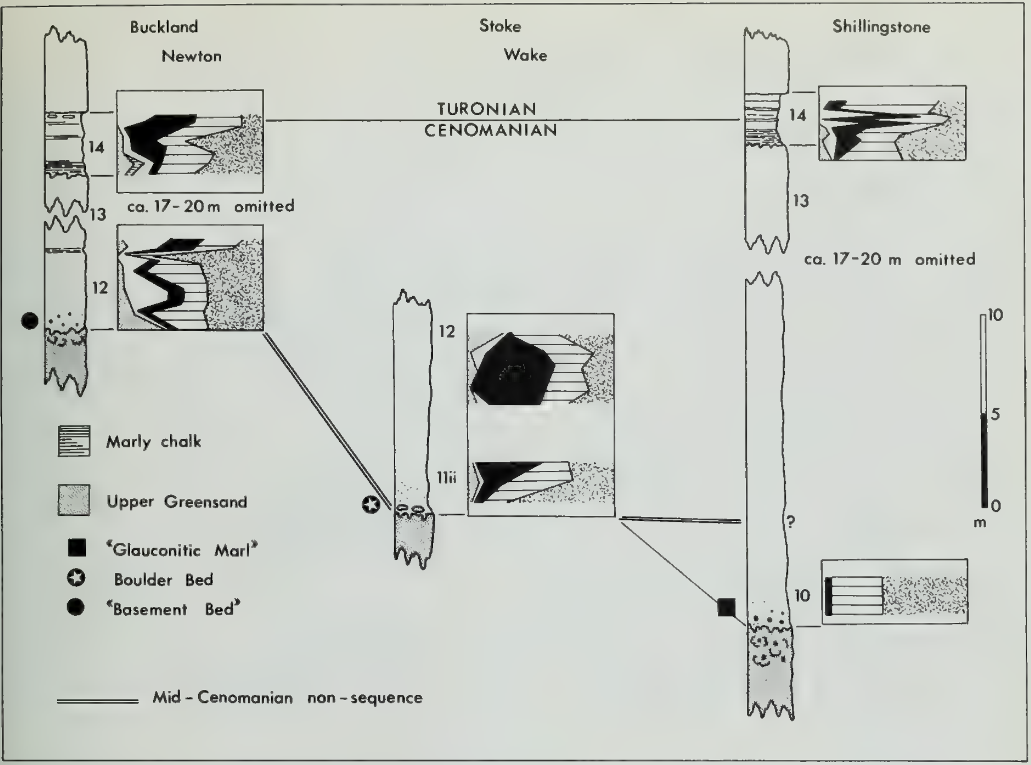


Fig. 15 The relationship between the mid-Cenomanian non-sequence and the Chalk Basement Bed in central Dorset. The ornament used in the planktonic/benthonic ratio graphs is explained in Fig. 12c.

Marssonella oxycona (Reuss) mimicking *M. ozawai* in the two cycles immediately preceding the non-sequence.

Returning to the model (Fig. 13), chalk deposition should continue above the non-sequence in the centre of the basin and, since the lithological changes would be slight, it could only be detected palaeontologically. However, on the margins of the basin a more dramatic sedimentological change would be expected. In these areas the calcareous sandstones (postulated in the model) would be replaced by Middle and Upper Cenomanian chalk, giving an easily recognizable horizon. It is not surprising that in Dorset the non-sequence becomes a feature of such importance that it dominates the whole of mid-Cretaceous stratigraphy in that area. The data concerning this level has been summarized by Kennedy (1970 : fig. 19) although no real explanation of the feature was given in his account. In Dorset (Fig. 14) there is a transition from an 'invisible' non-sequence into the prominent Chalk Basement Bed – with its rich fauna of phosphatized macrofossils. To the east of Stoke Wake (ST 763067) the Lower Chalk succession (Fig. 15) is normal, with a bed of 'glauconitic marl' at its base. This marl – as was explained by Carter & Hart in the discussion of Kennedy (1969) – is not the same age as the 'Glauconitic Marl' of the Folkestone section. The most suitable sequence for direct comparison is that at Shillingstone Lime Works (ST 824098) (Fig. 22, p. 77), where 42 m of chalk below the Plenus Marls has been recorded. A short distance to the south-east of the quarry the base of the chalk can be seen in the banks (ST 846106) of the River Stour (Kennedy 1970 : 622). The base of the chalk at this locality is completely different from that at Stoke Wake (Fig. 15) where a layer of large, glauconite-stained limestone cobbles marks the highly irregular contact. At Dorsetshire Gap (ST 742033) and Buckland Newton (ST 703051) the base of the chalk shows the Chalk Basement Bed. The graphs in Fig. 15 demonstrate

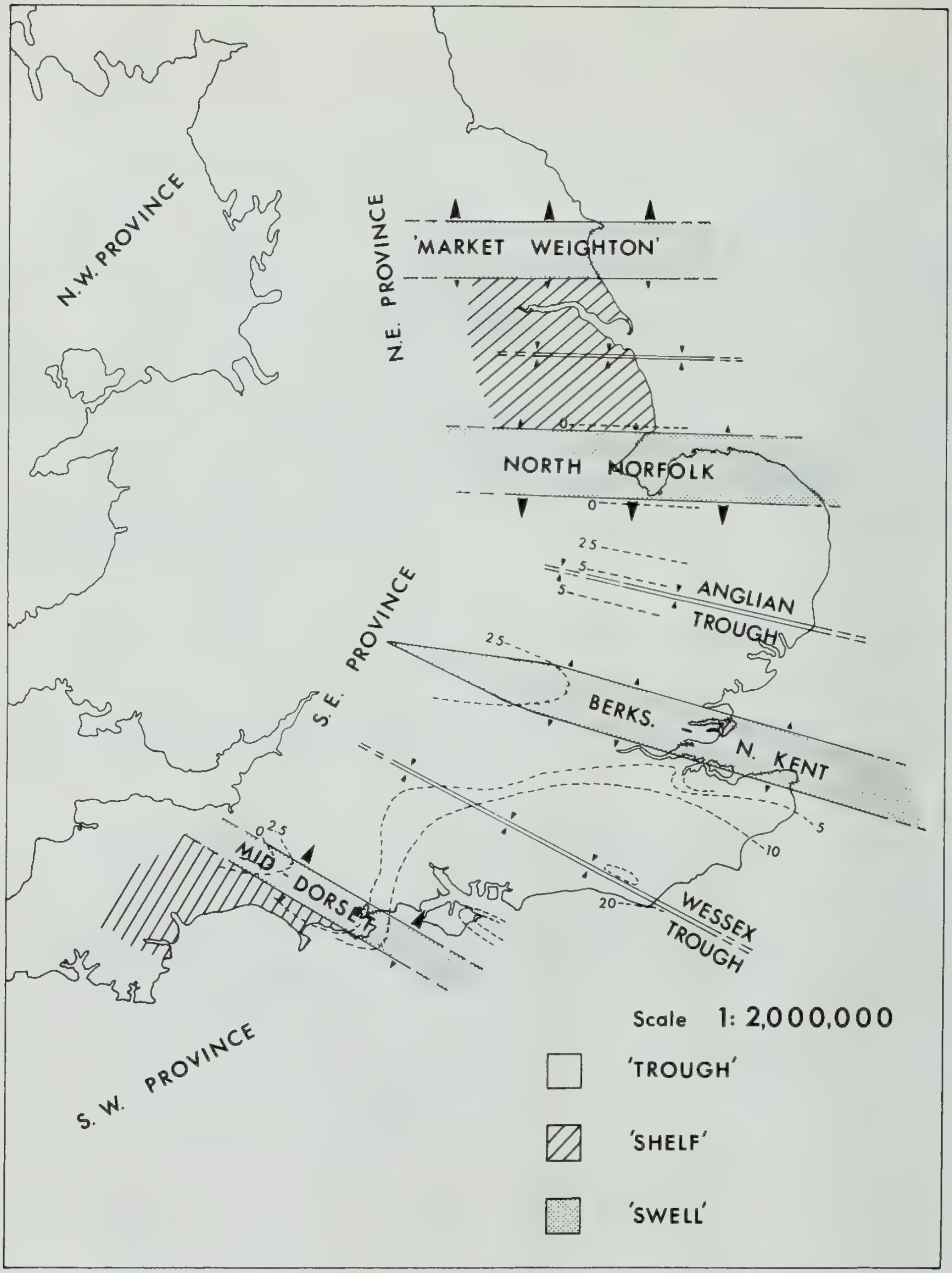

N.W. PROVINCE
N.E. PROVINCE
'MARKET WEIGHTON'
NORTH NORFOLK
0
0
2.5
5
5
ANGLIAN TROUGH
S.E. PROVINCE
2.5
BERKS. N. KENT
5
10
20
WESSEX TROUGH
0
2.5
MID DORSET
S.W. PROVINCE
Scale 1: 2,000,000
'TROUGH'
'SHELF'
'SWELL'

Fig. 16 Location of the major 'axes' affecting Lower Chalk sedimentation in England, and their relationship to the thickness of the *Actinocamax plenus* Marls. Isopachytes (in feet) based on the work of Jefferies (1963) and the present authors. These axes are also used in the delimitation of the provinces discussed in the stratigraphic account.

that west of Stoke Wake the mid-Cenomanian non-sequence is coincident with the base of the Chalk, while to the east of this locality the base of the chalk is below this level. The Chalk Basement Bed is therefore shown to be the visible expression of the mid-Cenomanian non-sequence. This phosphate conglomerate can be traced over the greater part of Dorset, as well as parts of Somerset and Devon, wherever the base of the chalk is exposed. The position of this feature in Devon is slightly complicated by the appearance of the Cenomanian Limestones, to be discussed in a later section. By plotting the base of the chalk (i.e. Basement Bed, nodule bed and glauconitic marl) it is possible to determine the areal relationship of these features. This is shown in Fig. 14. The appearance of the Basement Bed coincides with the already-described line of the Mid-Dorset Swell (Drummond 1970; Kennedy 1970), which indicates this feature persisted into the mid-Cenomanian, and even at this late stage was actively controlling sedimentation in the area. Jefferies (1963) has also attempted to show, somewhat indirectly, that the sedimentation of the Plenus Marls was also controlled by the same, or similar, basement structures. Jefferies' data, and the results of our own field work, are presented in Fig. 16 which shows how the isopachytes of the Plenus Marls reflect the presence of these 'basement structures'. The section between Dover, Eastbourne and the Isle of Wight (Fig. 19, p. 74) demonstrates the relationship between Plenus Marls sedimentation and the mid-Cenomanian non-sequence. It is interesting to note that the Plenus Marls succession is essentially uniform above the erosion surface at the base of Bed 4, the overall variations in thickness being largely due to variations in Beds 1–3. The main controlling influence on the sedimentation pattern is therefore Cenomanian and not Turonian as suggested by Jefferies (1963). The uniform nature of the succession above the Bed 3/Bed 4 boundary also adds weight to the suggestion that this level is the most suitable for the Cenomanian/Turonian boundary. The isopachyte map (Fig. 16) also can be used to delimit depositional trends which we will subsequently show are the most important features of the Cenomanian palaeogeography of the Anglo-Paris Basin. The map also can be used to delimit the following four provinces to be used in the stratigraphic analysis.

SE Province – characterized by the standard succession of the Gault Clay, Upper Greensand and Lower Chalk of normal depositional type.
SW Province – characterized by thick sequences of Upper Greensand, the absence of the true Gault Clay, the appearance of thin sandy limestones which are overlain by atypical chalk, which usually displays a marked phosphatic conglomerate at its base (the 'Chalk Basement Bed' of Kennedy (1970) and Drummond (1970)).
NE Province – characterized by a reduced Lower Chalk succession, red and pink chalks, nodular chalks and the 'Black Band' (Plenus Marls).
NW Province (including Antrim, the Inner Hebrides and Argyll) – characterized by thin glauconitic sands, overlain by pure glass sands and very thin, hard limestones (commonly recrystallized).

Stratigraphic analysis

Although much new information concerning the mid-Cretaceous of the British Isles is available no attempts at a comprehensive survey have been made. Specific topics have received detailed attention, but only Kennedy (1969, 1970) has provided a general account of the Lower Chalk over the whole of southern England. While his two papers give a detailed account of the sections visible in the field, he has made no attempt to synthesize his data. Kennedy's correlation diagrams (e.g. 1969 : fig. 16) do not fulfil our present requirements. In the example quoted above, some sections (e.g. Beddingham) are plotted at the opposite end of the diagram to those sections that are closest to them geographically. However, Kennedy's data on most of the sections used in this account is adequate and obviates the need for lengthy repetition.

The SE Province is discussed below as an introduction to the more detailed account of the south-west of England. The NE and NW Provinces have not been studied in the same detail and only short outline reports of those areas are given.

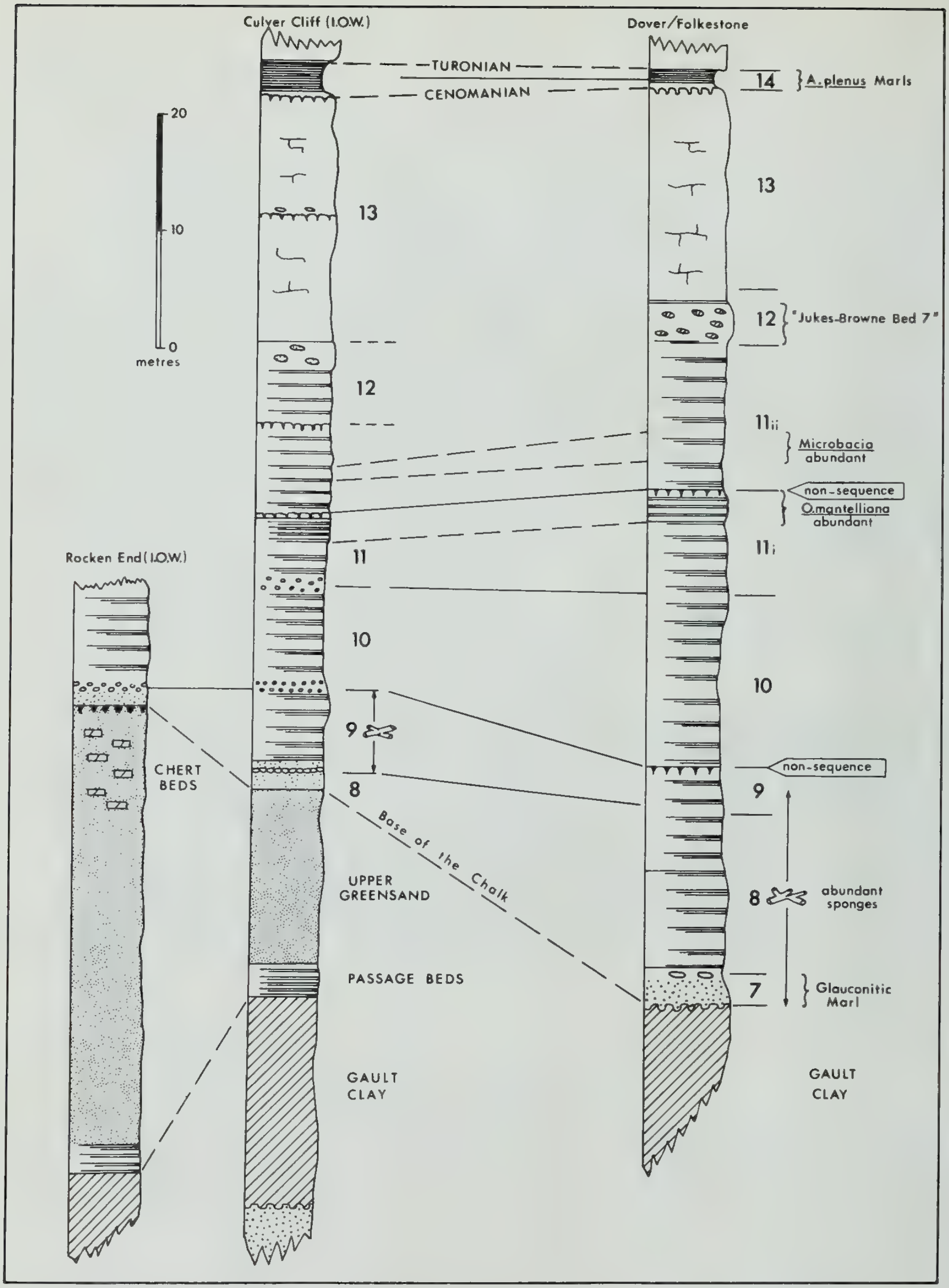

Culver Cliff (I.O.W.)
Dover/Folkestone
TURONIAN
CENOMANIAN
14
A. plenus Marls
20
10
0
metres
13
13
12
12
"Jukes-Browne Bed 7"
11ii
Microbacia abundant
non-sequence
O. mantelliana abundant
11
11i
Rocken End (I.O.W.)
10
10
CHERT BEDS
9
non-sequence
9
8
Base of the Chalk
UPPER GREENSAND
8
abundant sponges
PASSAGE BEDS
7
Glauconitic Marl
GAULT CLAY
GAULT CLAY

Fig. 17 The more important lithological features of the SE Province, together with the correlation of successions in Kent and the Isle of Wight.

a. South-east Province

This province consists of a single basin of deposition which continues across the English Channel into the Paris Basin. It is bordered by two distinct features, the Mid-Dorset Swell to the south-west and the North Norfolk Swell to the north. The central feature of the Berkshire – North Kent Swell, barely noticeable in central England, becomes more prominent in northern France.

As the more important lithological features of this area are already well known, Fig. 17 shows only three sections. Those shown illustrate the most important features encountered between Folkestone and the Isle of Wight.

i. The Plenus Marls succession remains constant in form and the individual beds and erosion surfaces (Jefferies 1962, 1963) are easily recognized.

ii. The mid-Cenomanian non-sequence cuts across the Lower Chalk succession, immediately above the *Orbirhynchia mantelliana* band.

iii. The relatively minor non-sequence at the Zone 9/Zone 10 boundary at Folkestone is marked in the Isle of Wight by a phosphate bed.

iv. The age of the base of the Lower Chalk varies between Dover and the Isle of Wight. At Culver Cliff the lowest beds correspond to a horizon well above the base of the Dover succession.

v. The Gault Clay passes westwards into the Upper Greensand succession.

vi. The Chert Beds appear only in the upper levels of the Upper Greensand, and in the SE Province are restricted to the southernmost tip of the Isle of Wight and the area around Warminster (Wiltshire).

The SE Province can best be described with reference to two cross-sections. The more important (Fig. 18) traverses southern England from Hunstanton in the north to Buckland Newton in the south. The more southerly profile from Folkestone/Dover to Swanage (Fig. 19, p. 74) relies on coastal exposures, although some borehole evidence has been incorporated. Although both sections are oblique to the main structural trends, the latter can nevertheless be determined. As already noted, the Berkshire – North Kent Swell is barely noticeable in Berkshire, and only becomes important across the Channel in France. However, it can be recognized by the change in lithology across it. The main sedimentological variations in the two subsidiary troughs and the intervening and marginal swells can be summarized as follows.

i. *Anglian Trough*

a. The Upper Greensand is very restricted, and found only in the south-west corner.
b. The Cambridge Greensand is seen at the base of the Lower Chalk in the centre of the trough.
c. Immediately below the mid-Cenomanian non-sequence there is a series of hard limestone beds, which suggest some degree of condensation.

ii. *Wessex Trough*

a. The Upper Greensand is well developed over the greater part of the area.
b. The Warminster Greensand occurs below the Lower Chalk in the centre of the trough.
c. The beds below the mid-Cenomanian non-sequence contain abundant *O. mantelliana*, but are of normal lithology.

iii. *The intervening and marginal swells*

On the northern margin of the Anglian Trough the Gault Clay and Lower Chalk successions are condensed and thin: on the southern margin of the Wessex Trough they have been much reduced by non-deposition or erosion. Over the Berkshire – North Kent Swell between the troughs the sequence is slightly reduced by losses immediately below the mid-Cenomanian non-sequence.

While the important breaks in the succession (sub-*plenus* surface, mid-Cenomanian, Zone 9/Zone 10, and the Albian/Cenomanian non-sequences) can be recognized in both troughs there are slight differences in their effects. In the Anglian Trough, and particularly in the vicinity of the North Norfolk Swell, the succession appears to be reduced in thickness more by condensation of

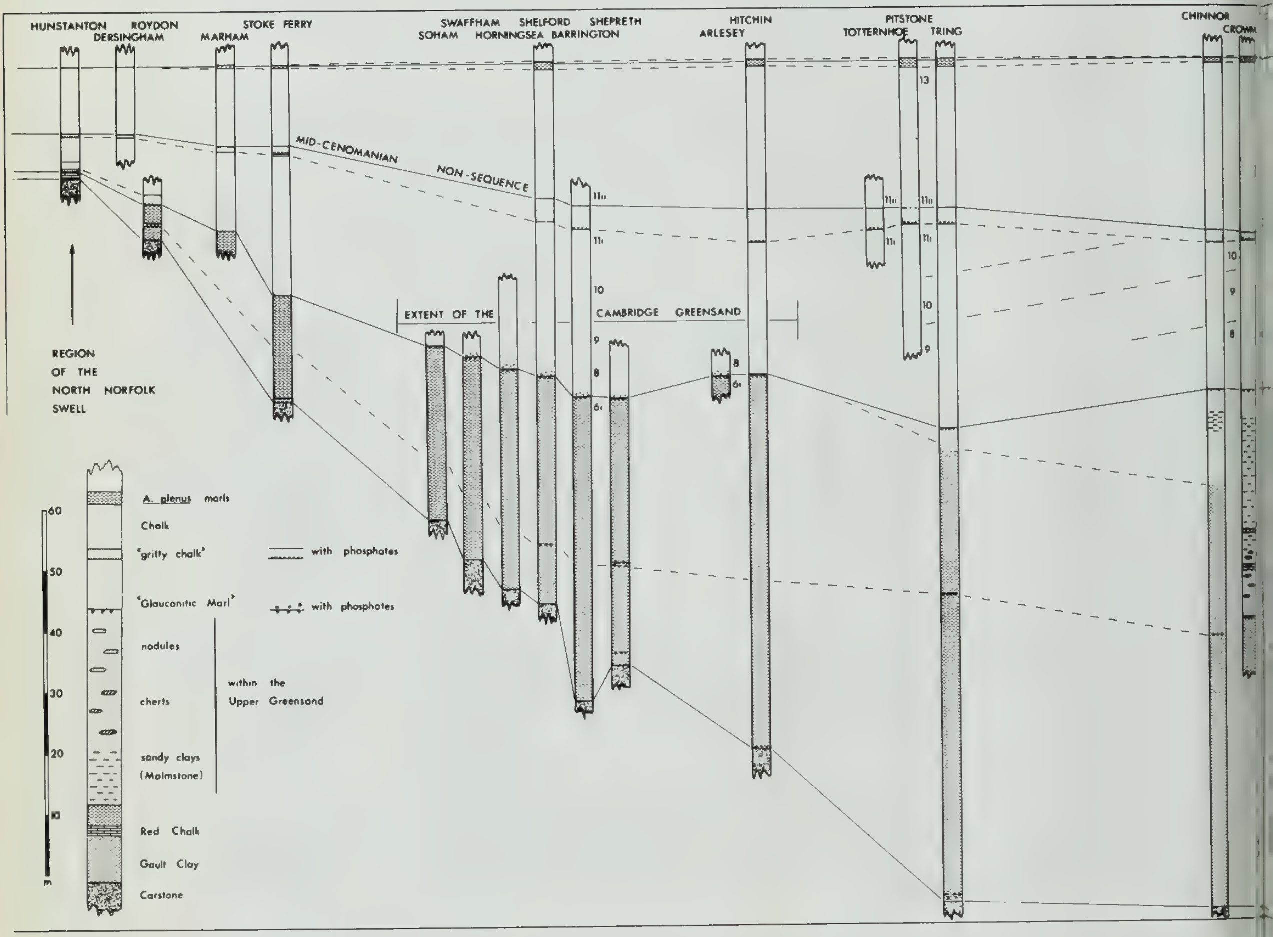
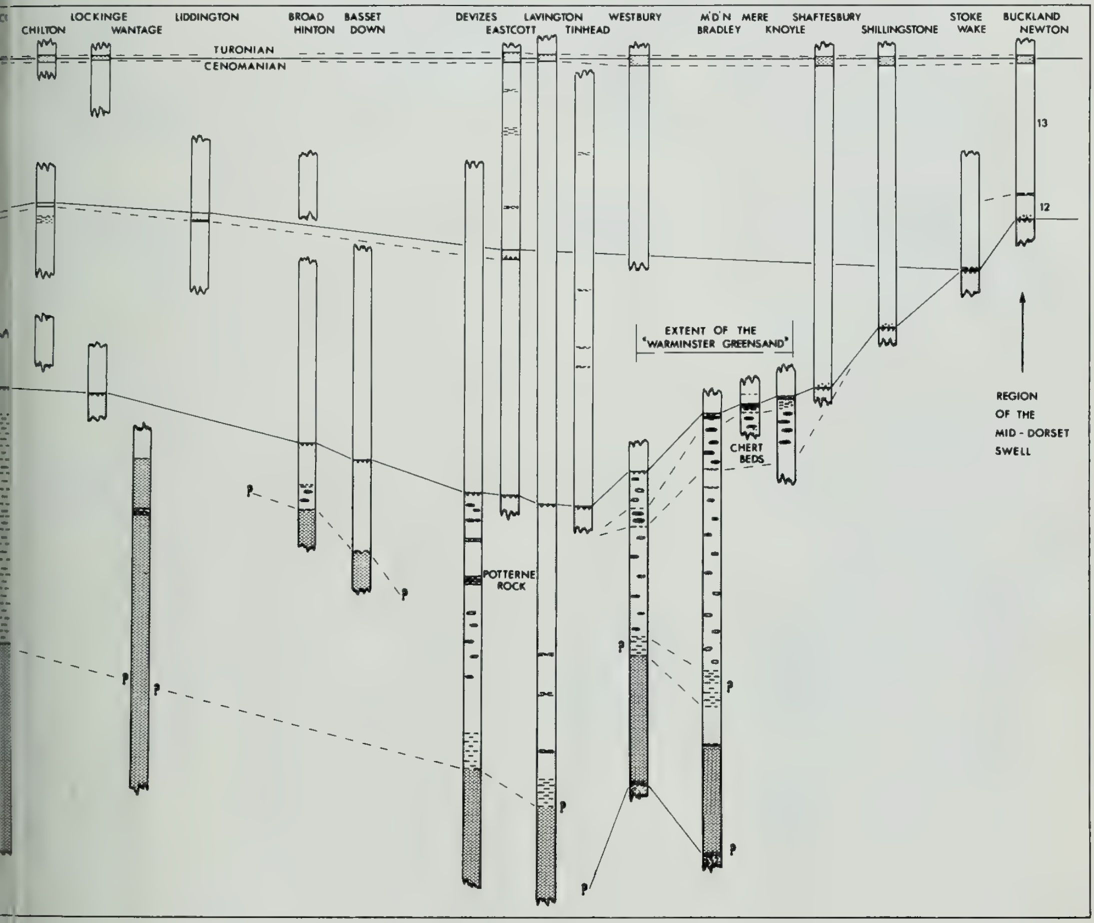

HUNSTANTON
ROYDON
DERSINGHAM
MARHAM
STOKE FERRY
SWAFFHAM
SOHAM
SHELFORD
HORNINGSEA
SHEPRETH
BARRINGTON
HITCHIN
ARLESEY
PITSTONE
TOTTERNHOE
TRING
CHINNOR
CROWM
MID-CENOMANIAN NON-SEQUENCE
EXTENT OF THE CAMBRIDGE GREENSAND
REGION OF THE NORTH NORFOLK SWELL
13
11ii
11i
10
9
8
6i
60
50
40
30
20
10
m
A. plenus marls
Chalk
'gritty chalk'
'Glauconitic Marl'
with phosphates
with phosphates
nodules
cherts
sandy clays (Malmstone)
within the Upper Greensand
Red Chalk
Gault Clay
Carstone

Fig. 18 The correlation of the mid-Cretaceous fr


CHILTON
LOCKINGE
WANTAGE
LIDDINGTON
BROAD HINTON
BASSET DOWN
DEVIZES
EASTCOTT
LAVINGTON
TINHEAD
WESTBURY
M'D'N BRADLEY
MERE
KNOYLE
SHAFTESBURY
SHILLINGSTONE
STOKE WAKE
BUCKLAND NEWTON
TURONIAN
CENOMANIAN
13
12
EXTENT OF THE 'WARMINSTER GREENSAND'
CHERT BEDS
POTTERNE ROCK
REGION OF THE MID - DORSET SWELL
?
?
?
?
?
?
?
?
?

ustanton (Norfolk) to Buckland Newton (Dorset).

the individual beds than by the removal or non-deposition of parts of the succession. The Wessex Trough, on the other hand, shows normal deposition over the whole area, with marked reductions of overall thickness caused by erosion or non-deposition, or both. This is demonstrated when the style of deposition on the two boundary swells is compared. These differences persist beyond the confines of the SE Province; the whole of the NE Province is dominated by condensed successions, while the SW Province successions show prominent erosion surfaces.

The stratigraphy of the SE Province will now be considered by regions.

1. *The margin of the North Norfolk Swell*

It is unfortunate that micropalaeontological control is so poor in the area bordering the North Norfolk Swell. This is due to a combination of poor exposure, difficult lithology and as yet incomplete sampling of that area. At present only an indication of the trends in this area can be given. Hunstanton is on the edge of a shelf, south of which all parts of the succession expand rapidly in thickness. This is particularly true of the Gault Clay, although the thickening of the Lower Chalk is also striking. However, both units are incomplete, even in the centre of the Anglian Trough.

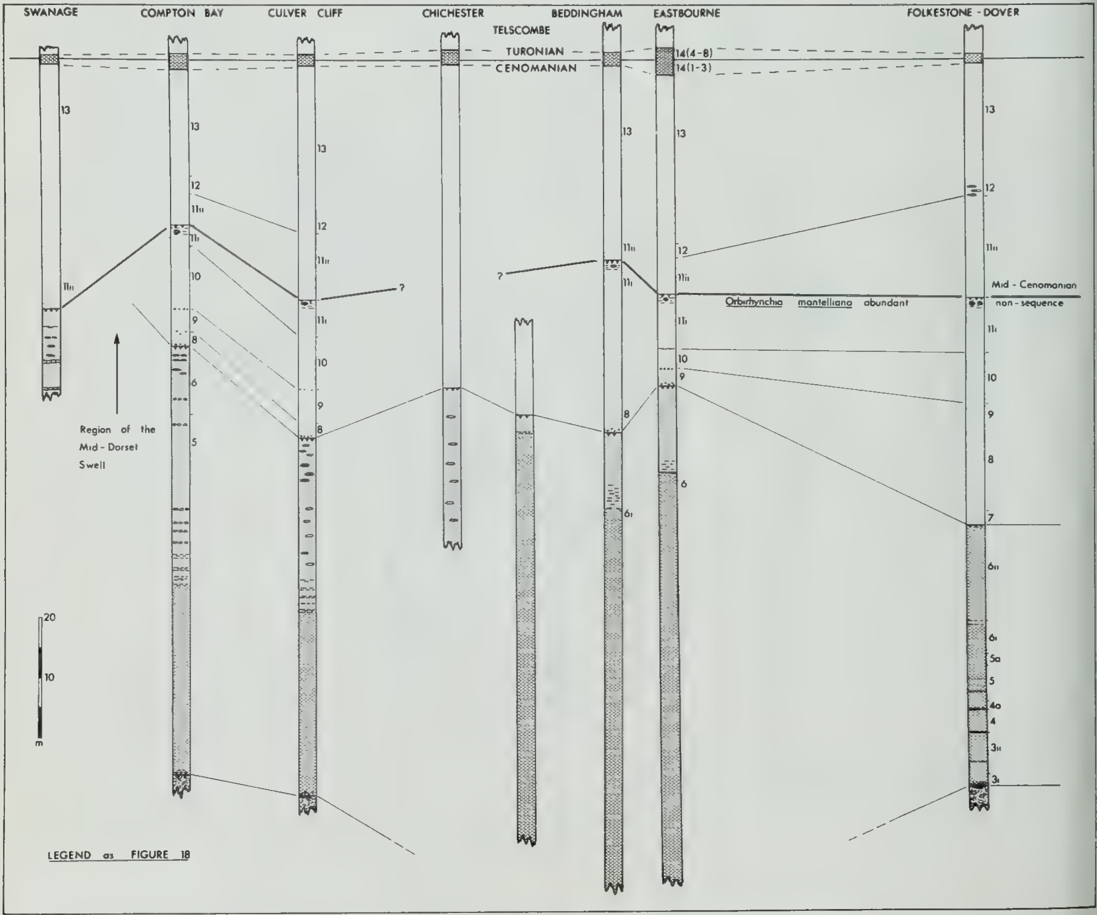

SWANAGE
COMPTON BAY
CULVER CLIFF
CHICHESTER
BEDDINGHAM
EASTBOURNE
FOLKESTONE - DOVER
TELSCOMBE
TURONIAN
CENOMANIAN
14(4-8)
14(1-3)
13
12
11ii
11i
10
9
8
7
6
6i
6ii
5
5a
4
4a
3i
3ii
?
Region of the Mid-Dorset Swell
Orbirhynchia mantelliana abundant
Mid - Cenomanian non - sequence
20
10
m
LEGEND as FIGURE 18

Fig. 19 The correlation of the mid-Cretaceous from Dover (Kent) to Swanage (Dorset). (The Eastbourne succession has provided several workers (e.g. Kennedy 1969) with a problem, and the thickness used in this account is one of many recent estimates. Faulting has completely broken up the lower levels of the sequence.)

2. *The Anglian Trough*

In this area the base of the Lower Chalk is represented by the Cambridge Greensand (Hart 1973a). Detailed microfaunal analysis has shown that the age of the Cambridge Greensand is upper Zone 8 (uppermost *Hypoturrilites carcitanensis* Assemblage Zone of Kennedy 1969), even though the only dateable macrofaunal elements are from the *dispar* Zone. The underlying Gault Clay belongs, on microfaunal grounds, to the *Arrhaphoceras substuderi* Subzone of the *dispar* Zone. This shows that the upper part of the *dispar* Zone is not represented in this part of Cambridgeshire, even

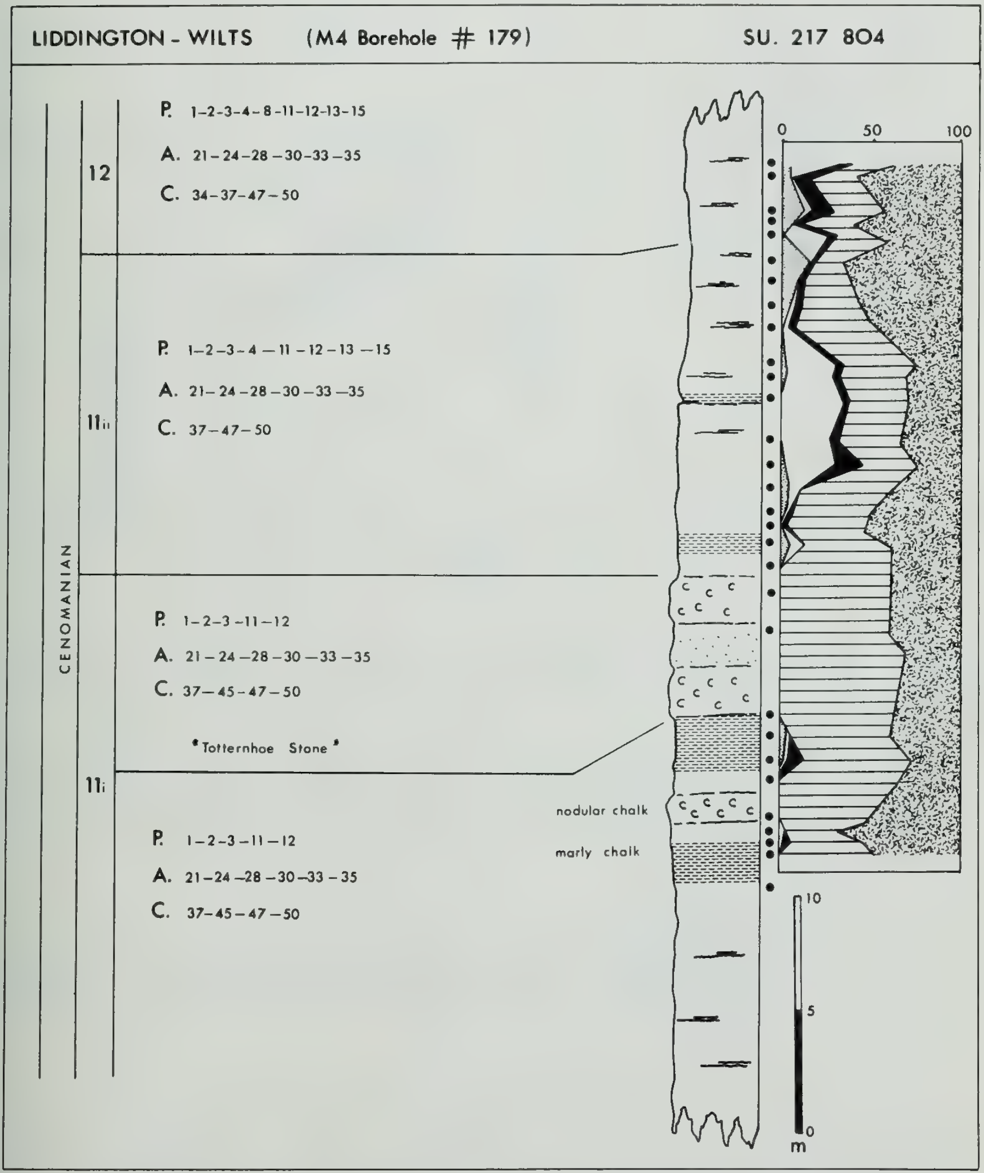

LIDDINGTON - WILTS
(M4 Borehole # 179)
SU. 217 804
CENOMANIAN
12
P. 1-2-3-4-8-11-12-13-15
A. 21-24-28-30-33-35
C. 34-37-47-50
11ii
P. 1-2-3-4 — 11 - 12 - 13 — 15
A. 21-24-28-30-33-35
C. 37-47-50
P. 1-2-3-11-12
A. 21-24-28-30-33-35
C. 37-45-47-50
'Totternhoe Stone'
11i
P. 1-2-3-11-12
A. 21-24-28-30-33-35
C. 37-45-47-50
nodular chalk
marly chalk
0
50
100
10
5
0
m

Fig. 20 Microfaunal details, Liddington Borehole, Wiltshire. The ornament used in the planktonic/benthonic ratio graph is explained on Fig. 12c. The species lists are in three categories (P. – planktonic, A. – agglutinated benthonic and C. – calcareous benthonic), the numbers referring to the species listed on the range chart (Fig. 9). The black dots indicate sample positions in all vertical sections.

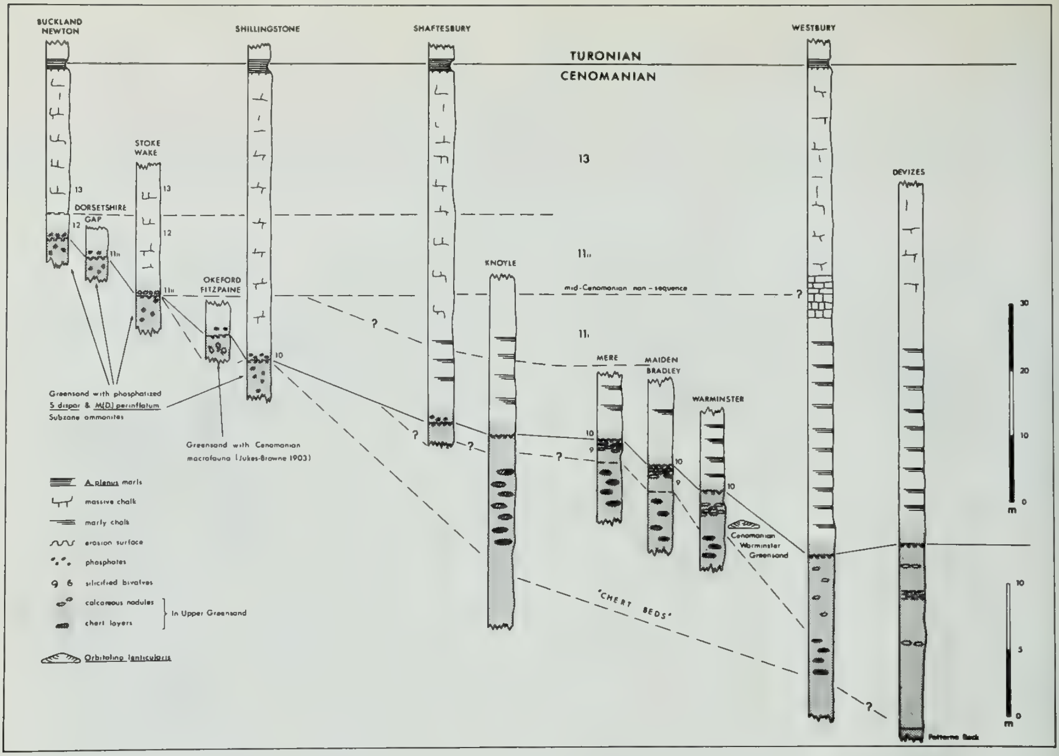

BUCKLAND NEWTON
SHILLINGSTONE
SHAFTESBURY
WESTBURY
TURONIAN
CENOMANIAN
13
STOKE WAKE
DEVIZES
13
DORSETSHIRE GAP
12
11ii
11ii
OKEFORD FITZPAINE
11ii
KNOYLE
mid-Cenomanian non-sequence
?
11i
10
?
MERE
MAIDEN BRADLEY
WARMINSTER
Greensand with phosphatized S dispar & M(D) perinflatum Subzone ammonites
Greensand with Cenomanian macrofauna (Jukes-Browne 1903)
10
9
10
9
10
Cenomanian Warminster Greensand
?
?
?
'CHERT BEDS'
?
Potterne Rock
30
20
10
0
m
10
5
0
m
A. plenus marls
massive chalk
marly chalk
erosion surface
phosphates
silicified bivalves
calcareous nodules
chert layers
In Upper Greensand
Orbitolina lenticularis

Fig. 21 The correlation of the mid-Cretaceous from Devizes (Wiltshire) to Buckland Newton (Dorset).

though its fauna can be collected from the famous 'coprolite bed'. The relationship between an absent *dispar* Zone and an overlying bed containing *dispar* faunal elements is discussed in the section on the SW Province.

The other characteristic feature of the Anglian Trough is the presence of the Totternhoe Stone (Chilton Stone, Burwell Rock) immediately below the mid-Cenomanian non-sequence. The relationship between this lithological unit and the non-sequence has already been described (p. 66). The distribution of this bed is shown in Fig. 18, and the succession above it in the Liddington borehole in Fig. 20.

3. *The Berkshire – North Kent Swell*

At present little is known about the sequences in this area. Work in progress indicates a large hiatus below the mid-Cenomanian non-sequence in west central Buckinghamshire, but the Albian–Cenomanian boundary has not yet been studied.

4. *The Wessex Trough* (*North-western Region*)

At present very little information is available concerning the base of the Lower Chalk and the fauna of the Upper Greensand from the area between Chinnor and Warminster. This region has not been studied in the same detail as south Wiltshire and north Dorset. However, Kelly (1971) recorded Albian ammonites from the Upper Greensand at Edington (Wiltshire). Spath (1923–43) demonstrated that the Potterne Rock contained a rich, non-phosphatized ammonite fauna of *Callihoplites auritus* Subzone age, while above this horizon the 30 m of glauconitic sands yielded elements from the *Stoliczkaia dispar* Zone. At Edington, Kelly records a phosphatized fauna of

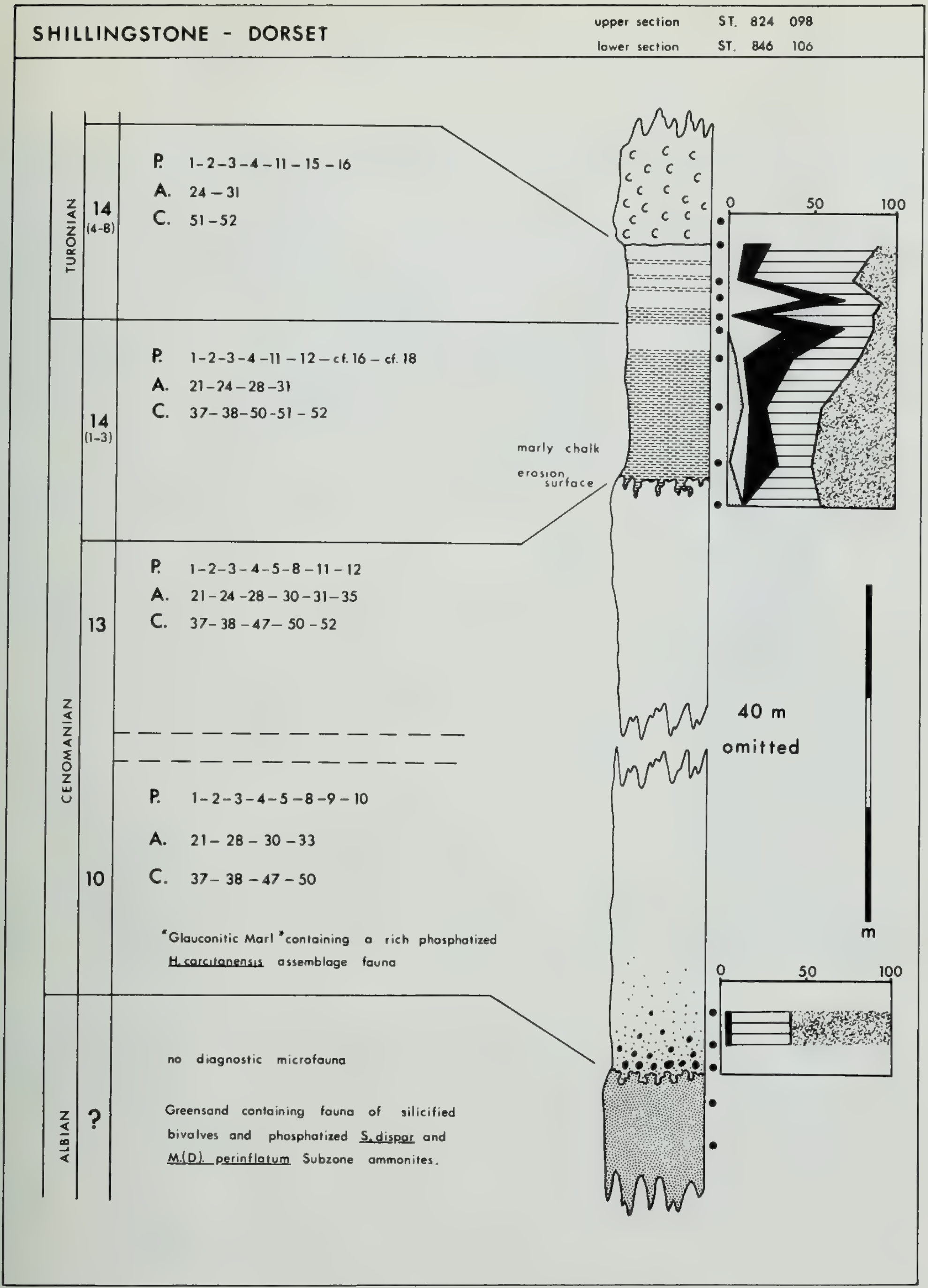

SHILLINGSTONE - DORSET
upper section ST. 824 098
lower section ST. 846 106
TURONIAN
14
(4-8)
P. 1-2-3-4-11-15-16
A. 24-31
C. 51-52
14
(1-3)
P. 1-2-3-4-11-12-cf. 16-cf. 18
A. 21-24-28-31
C. 37-38-50-51-52
marly chalk
erosion surface
CENOMANIAN
13
P. 1-2-3-4-5-8-11-12
A. 21-24-28-30-31-35
C. 37-38-47-50-52
40 m
omitted
10
P. 1-2-3-4-5-8-9-10
A. 21-28-30-33
C. 37-38-47-50
"Glauconitic Marl" containing a rich phosphatized H. carcitanensis assemblage fauna
ALBIAN
?
no diagnostic microfauna
Greensand containing fauna of silicified bivalves and phosphatized S. dispar and M.(D). perinflatum Subzone ammonites.
0
50
100
0
50
100
m

Fig. 22 Microfaunal details, Shillingstone, Dorset. The ornament used in the planktonic/benthonic graph is explained in Fig. 12c; the letter code in Fig. 20.

the *auritus* Subzone, while the rarer, non-phosphatized elements of the fauna indicate a slightly younger horizon. No microfaunal information is available from here.

5. *The margin of the Mid-Dorset Swell*

Since important changes occur adjacent to the Mid-Dorset Swell the area between Warminster and Buckland Newton has been studied in considerable detail. In this region (Fig. 21) the Lower Chalk thins from approximately 60 m in the Westbury area to about 25–30 m in mid-Dorset. Unfortunately, the all-important mid-Cenomanian non-sequence is not exposed and the lithological sequences must be constructed without reference to one of the more important datum levels within the Lower Chalk. As the thickness of the Lower Chalk is known at several localities some information can be gleaned from the age determinations of the lowest levels. At all the localities studied (Stour Bank (ST 846106, Fig. 22), Mere (ST 804323, Fig. 23) and Maiden Bradley (ST 797390, Fig. 24)) the basal, glauconitic chalk yields a Zone 10 microfauna, although the precise position within that zone cannot be determined. The sequence below this zone is highly complex, and contains a series of boulder or 'popple' beds, greensands, and greensands with

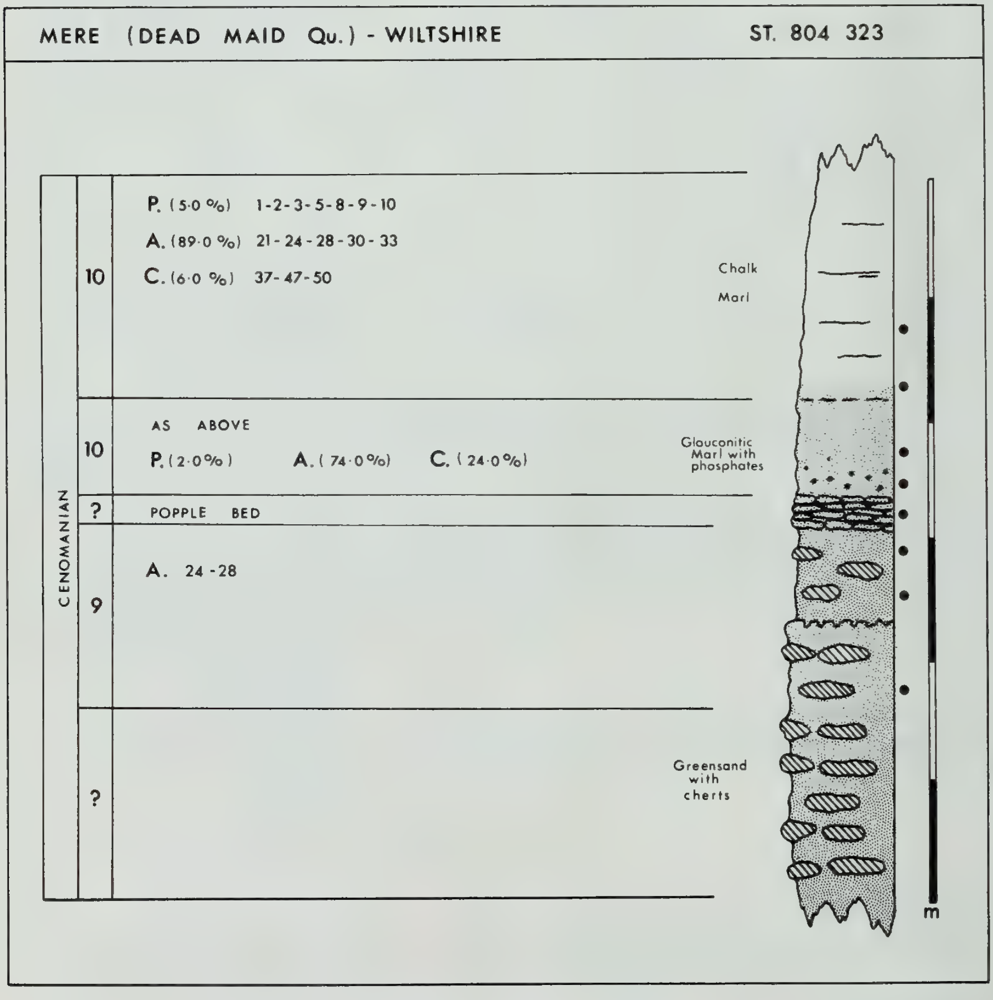

MERE (DEAD MAID Qu.) - WILTSHIRE
ST. 804 323
CENOMANIAN
10
P. (5·0 %) 1-2-3-5-8-9-10
A. (89·0 %) 21-24-28-30-33
C. (6·0 %) 37-47-50
Chalk Marl
10
AS ABOVE
P. (2·0%) A. (74·0%) C. (24·0%)
Glauconitic Marl with phosphates
?
POPPLE BED
9
A. 24-28
?
Greensand with cherts
m

Fig. 23 Microfaunal details, Dead Maid Quarry, Mere, Wiltshire. See Fig. 20 for explanation of letter code.

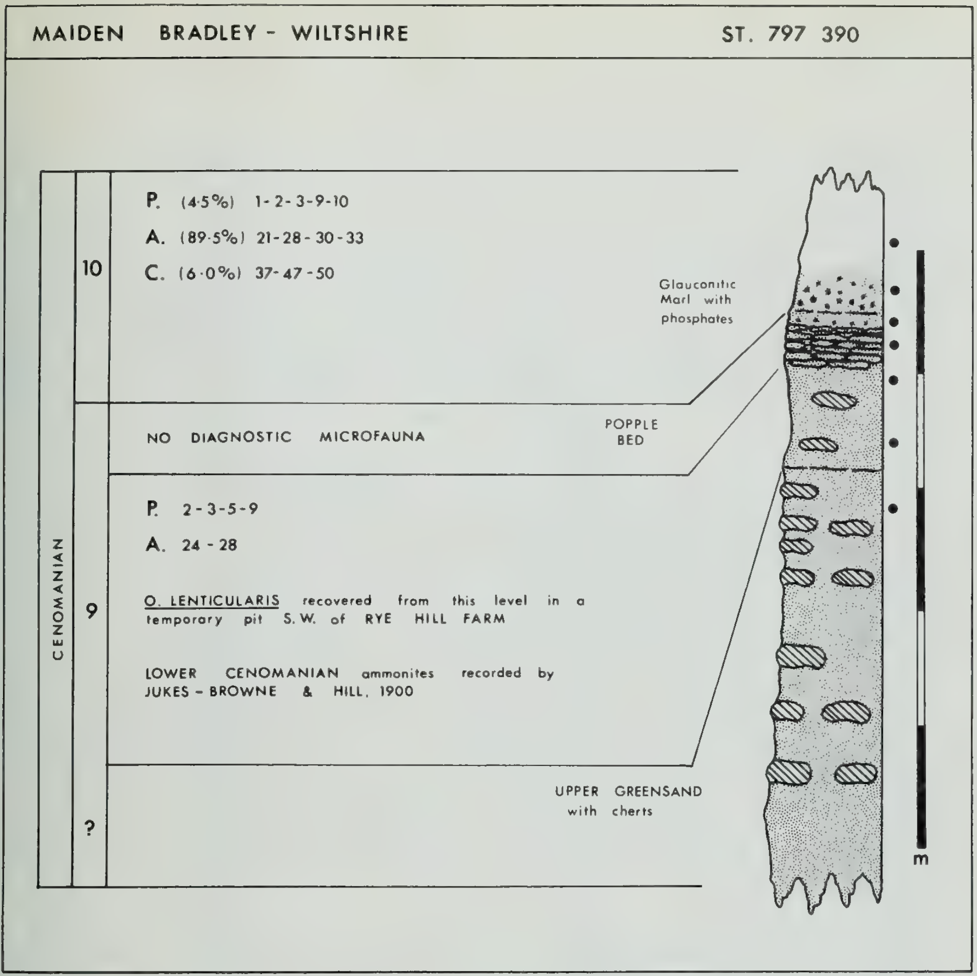

MAIDEN BRADLEY - WILTSHIRE
ST. 797 390
P. (4·5%) 1-2-3-9-10
A. (89·5%) 21-28-30-33
C. (6·0%) 37-47-50
10
NO DIAGNOSTIC MICROFAUNA
P. 2-3-5-9
A. 24 - 28
O. LENTICULARIS recovered from this level in a temporary pit S.W. of RYE HILL FARM
LOWER CENOMANIAN ammonites recorded by JUKES - BROWNE & HILL, 1900
CENOMANIAN
9
?
Glauconitic Marl with phosphates
POPPLE BED
UPPER GREENSAND with cherts
m

Fig. 24 Microfaunal details, Maiden Bradley, Wiltshire. See Fig. 20 for explanation of letter code.

cherts. The most important lithological unit is the Warminster Greensand, with its well-known Lower Cenomanian fauna (Jukes-Brown & Hill 1900 : 238). This greensand, and its lateral equivalent the Rye Hill Sand, is extremely poor in microfossils although Dr P. V. O. Drummond has presented us with a magnificent specimen of *Orbitolina lenticularis* (Blumenbach) washed from a temporary exposure in the greensand. In this area the underlying chert-bearing greensand has yielded no diagnostic macrofossils (Jukes-Browne & Scanes 1901, Edmunds 1938, Kennedy 1970). The age of the base of the Chalk (Zone 10) given by the microfauna appears to conflict with the ammonite dating of Kennedy (1970 : 620), who records a Lower Cenomanian fauna, probably earlier than the main *saxbii* assemblage fauna of south-east England. While Cenomanian sands are also present below the base of the Chalk at Knoyle Corner (ST 897307) and Melbury Down (ST 875207) (Jukes-Brown & Hill 1900 : 160–161; 1903 : 104–105; Mottram, Hancock & House 1956), there must be a distinct change before the River Stour is reached at Stour Bank (ST 846106). At this locality the uppermost Upper Greensand is a complex bed of glauconitized cobbles set in softer greensand. There is an abundant macrofauna of silicified and phosphatized bivalves and ammonites. The 'glauconitic marls' which overlie this bed contain a very rich phosphatized fauna (Kennedy 1970 : 623) and an unphosphatized one belonging to the *carcitanensis* Assemblage

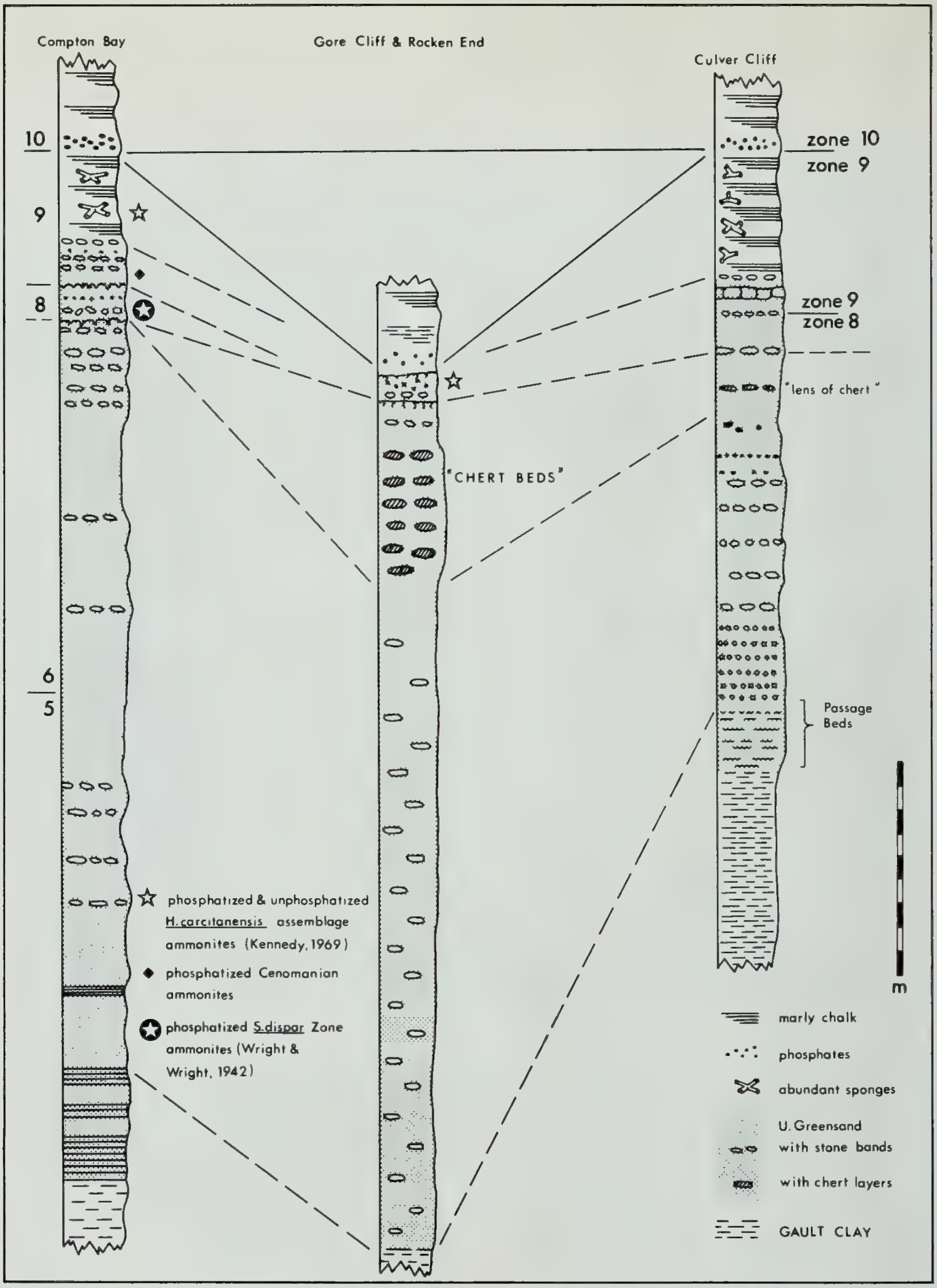

Compton Bay
Gore Cliff & Rocken End
Culver Cliff
10
9
8
6
5
zone 10
zone 9
zone 9
zone 8
"lens of chert"
"CHERT BEDS"
Passage Beds
m
phosphatized & unphosphatized H. carcitanensis assemblage ammonites (Kennedy, 1969)
phosphatized Cenomanian ammonites
phosphatized S. dispar Zone ammonites (Wright & Wright, 1942)
marly chalk
phosphates
abundant sponges
U. Greensand
with stone bands
with chert layers
GAULT CLAY

Fig. 25 A correlation of the Lower Cenomanian and Upper Albian successions of the Isle of Wight.

Subzone. This locality is interesting as it is one of the places in south-west England where a *S. dispar* Zone fauna is found within the Upper Greensand. The phosphatized fauna, with its associated silicified bivalves, can also be found at Dorsetshire Gap (ST 742033) and Buckland Newton (ST 703051). Its preservation and concentration must indicate that it is a reworked deposit. Its position is somewhat analogous to that of the phosphatized *S. dispar* Zone fauna found in the Upper Greensand below the Chert Beds on the Purbeck coast (Fig. 45, p. 103), and that of the *S. dispar* Zone fauna from the upper levels of the Upper Greensand succession in the Isle of Wight. It is important to note that the basal beds of the Chalk in the Stour Valley do not contain elements of an Albian fauna, the latter being completely within the Upper Greensand. If this faunal distribution is compared with that seen in Cambridgeshire, clearly there are some important differences. In Cambridgeshire, the phosphatized *S. dispar* Zone fauna is found within the Chalk succession, above the major non-sequence of that area. As the lowermost Chalk at Stour Bank occupies a position above the Zone 9/Zone 10 non-sequence, there is a considerable gap in the succession between the basal Chalk and the underlying (?) uppermost Albian Upper Greensand. It follows also that the Chert Beds (see Fig. 21) are of post-*S. dispar* Zone age.

The Isle of Wight is in a similar position relative to the Mid-Dorset Swell as are south Wiltshire and north Dorset. The general section across it (see Fig. 19) requires some amplification. Unfortunately both the microfaunal and macrofaunal dating is inconclusive. A summary of the available data from both fields is shown on three sections in Fig. 25. The most important feature is the phosphate bed, which coincides with the Zone 9/Zone 10 boundary. This marks a non-sequence, which can be shown to be diachronous from south to north over the island and equates with that forming the base of the Chalk in the Warminster area. A few metres below the phosphate conglomerate at Compton Bay, in the uppermost Upper Greensand, occurs the phosphatized Upper Albian (*S. dispar* Zone) fauna described by Wright & Wright (1942), in a similar position to that recorded from Dorsetshire Gap and Stour Bank. This fauna occurs on this side of the Mid-Dorset Swell when the Chert Beds are found in the succession. The base of the 'glauconitic marl', both at Culver Cliff and Compton Bay, is in the upper levels of Zone 8 – well up in the Lower Cenomanian, at about the same level as the base of the Chalk in the Cambridgeshire area.

If the phosphatized *S. dispar* Zone fauna, seen at Compton Bay, is from a stratigraphically lower horizon than the chert-rich sequence, then this horizon, though undated, is identical with that found in south Wiltshire.

6. *The Wessex Trough* (*South-eastern Region*)

The greater part of the Lower Chalk succession can be correlated along the south coast towards Dover with little difficulty. The only problem is the dating of the Upper Greensand and the base of the Chalk. Although no diagnostic fossils have been found in the topmost levels of the Gault Clay or the overlying Upper Greensand, at Eastbourne the highest levels of the Gault Clay are thought to fall within the *inflatum* Zone (Kennedy 1967 : 368; 1969 : 504). The 'glauconitic marl' contains abundant, phosphatized *carcitanensis* Assemblage Subzone faunal elements as well as an unphosphatized fauna of the same assemblage. The bed of phosphatized ammonite just above this level correlates with that on the Isle of Wight at the Zone 9/Zone 10 boundary. This agrees with a Zone 9 age for the 'glauconitic marl'. The microfauna of the Upper Greensand on the foreshore at Beachy Head is not diagnostic and the junction with the Gault Clay is so broken up and confused that the dating of the clay as Zone 6 has little bearing on that of the greensand. However, the nearby Beddingham Limeworks (TQ 440093–440062) does provide a more complete and essentially less complicated succession. In the large pit near the railway line about 12–15 m of blue, sandy clay can be seen to become more silty and glauconitic when traced up the sequence. The transition into the Upper Greensand is very gradual and the boundary is very difficult to place. The results of our Beddingham investigations are shown in Fig. 26. The Gault Clay/Upper Greensand transition contains a Zone 6 fauna, but the recorded species indicate that it belongs to the lower levels of the zone. The presence of *Globigerinelloides bentonensis* in large numbers supports this determination – floods of this species are also found in the Gault Clay below the Cambridge Greensand, where the upper subzone of the *S. dispar* Zone is missing.

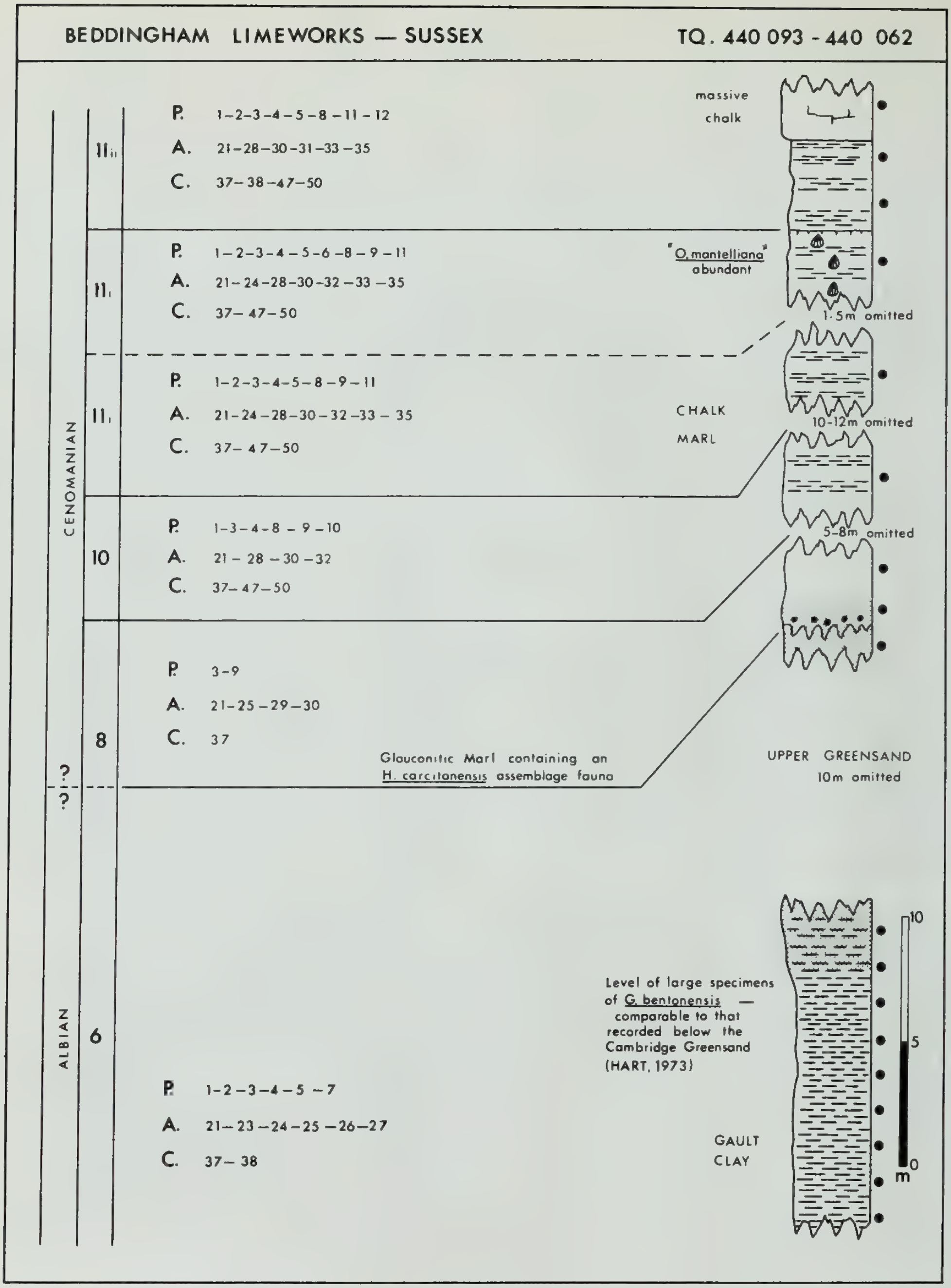

BEDDINGHAM LIMEWORKS — SUSSEX
TQ. 440 093 - 440 062
CENOMANIAN
ALBIAN
?
?
11ii
P. 1-2-3-4-5-8-11-12
A. 21-28-30-31-33-35
C. 37-38-47-50
11i
P. 1-2-3-4-5-6-8-9-11
A. 21-24-28-30-32-33-35
C. 37-47-50
11i
P. 1-2-3-4-5-8-9-11
A. 21-24-28-30-32-33-35
C. 37-47-50
10
P. 1-3-4-8-9-10
A. 21-28-30-32
C. 37-47-50
8
P. 3-9
A. 21-25-29-30
C. 37
6
P. 1-2-3-4-5-7
A. 21-23-24-25-26-27
C. 37-38
massive
chalk
"O. mantelliana"
abundant
1·5m omitted
CHALK
MARL
10-12m omitted
5-8m omitted
Glauconitic Marl containing an
H. carcitanensis assemblage fauna
UPPER GREENSAND
10m omitted
Level of large specimens
of G. bentonensis —
comparable to that
recorded below the
Cambridge Greensand
(HART, 1973)
GAULT
CLAY
10
5
0
m

Fig. 26 Microfaunal details, Beddingham Limeworks, nr Lewes, Sussex. See Fig. 20 for explanation of letter code.

The uppermost Upper Greensand contains the same fauna, and this shows that the uppermost Albian is wanting in this area. The fauna from the base of the overlying 'glauconitic marl' contains elements from the upper levels of Zone 8 (*Flourensina intermedia*, *Marssonella ozawai*, *Arenobulimina advena*, *Plectina mariae*, etc.) which are from slightly lower in the succession than on the coast only a few km away. The upper levels of the 'glauconitic marl' at Beddingham (Kennedy 1969 : 501) contain a sparse *carcitanensis* Assemblage fauna. As Zones 7 and 8 are thought to equate with this assemblage subzone there is no dispute between the microfauna and the macrofauna at this locality. As at Barrington (Cambridgeshire) a substantial thickness of the Lower Cenomanian is not represented, and so the situation in both the Anglian and Wessex Troughs is remarkably similar. The main difference is the absence of the derived, phosphatized *S. dispar* Zone elements from the more southerly of the two troughs.

The Folkestone succession, used as the standard for the Lower Chalk and Gault Clay, is relatively uncomplicated. The zonal chart (Fig. *a*, p. 53) has been based on this sequence. The Dover succession has also been used to demonstrate the use of the planktonic-benthonic ratio graphs in the Lower Chalk and its correlation with that recorded from the Betchworth Limeworks (TQ 207517) (see Fig. 12). The series of disused pits at Betchworth was studied in detail by Diver (1968), Bigg (1968) and Jaworski (1968). The succession exposed is rendered additionally useful by its proximity to the Fetcham Mill Borehole (Gray 1965). The succession in this borehole below the Plenus Marls is seen to correlate precisely with that described by Diver (1968), and the thickness of the 'glauconitic marl' compares favourably with the values obtained by Jaworski (1968). The 'glauconitic marl' belongs in Zone 9 while the overlying Chalk is of Zone 10 age. The Upper Greensand contains a Zone 7 or Zone 8 fauna, which places it within the Lower Cenomanian. This determination agrees with the evidence from the Fetcham Mill Borehole in which the first identifiable ammonite of Albian age, *Pleurohoplites* cf. *subvarians* Spath, does not occur until a

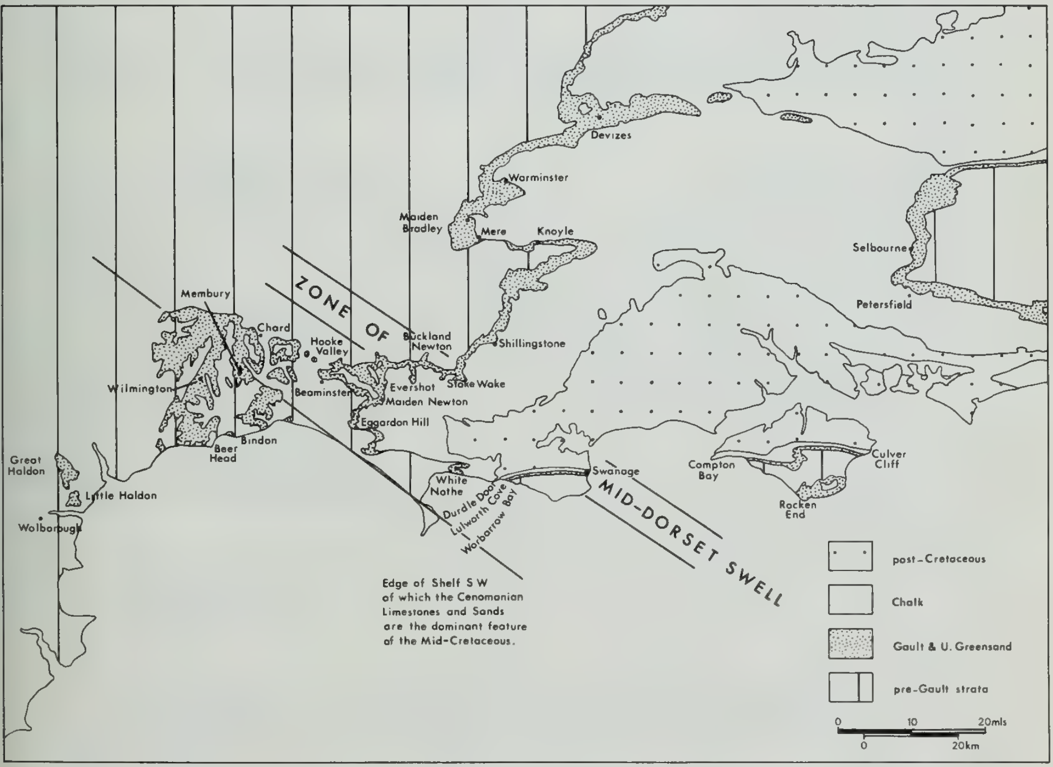

Devizes
Warminster
Maiden Bradley
Mere
Knoyle
Selbourne
Petersfield
Membury
ZONE OF
Chard
Hooke Valley
Buckland Newton
Shillingstone
Wilmington
Beaminster
Evershot
Stoke Wake
Maiden Newton
Eggardon Hill
Bindon
Beer Head
Great Haldon
Little Haldon
Wolborough
White Nothe
Durdle Door
Lulworth Cove
Worbarrow Bay
Swanage
MID-DORSET SWELL
Compton Bay
Culver Cliff
Rocken End
Edge of Shelf S W of which the Cenomanian Limestones and Sands are the dominant feature of the Mid-Cretaceous.
post-Cretaceous
Chalk
Gault & U. Greensand
pre-Gault strata
0
10
20mls
0
20km

Fig. 27 The more important localities and geological features of the south-west Province.

depth of 883′1″ (269·16 m) (with *Lephoplites* cf. *pseudoplanus* Spath at 883′2″ (269·19 m) and *Callihoplites* cf. *tetragonus* (Seeley) at 895′2″ (272·85 m)). This fauna is from the *substuderi* Subzone of the *S. dispar* Zone, and not (Casey *in* Gray 1965, Appendix B: 105) from the higher *perinflatum* Subzone. This ammonite evidence and the last record of *Schloenbachia* sp. at 840′11″ (256·31 m), within the 'glauconitic marl', was taken into account when plotting the base of the Cenomanian. A sample from above the 'glauconitic marl' from the borehole at depth 834′–835′ (c. 254·36 m) was studied by M. B. H. and shown to contain a fauna that places it close to the Zone 9/Zone 10 boundary. Another sample from 854′–855′ (c. 260·45 m) contains transitional forms between *Arenobulimina chapmani* and *A. advena* and must be from close to the Albian/Cenomanian boundary – possibly from Zone 6a. There is thus strong evidence for a Cenomanian age for some of the Upper Greensand in Surrey. An extensive study of the Gault Clay in Kent and Surrey is now in progress and this should help to determine the zonal position of the Upper Greensand where it first appears in the succession near Westerham. Work already completed confirms the Zone 8/Zone 9 dating for the base of the Lower Chalk throughout the larger part of south-east England. The succession in Kent is therefore the only one that displays a relatively complete Lower Chalk succession, although even in that area there are horizons where some removal of material is suspected.

The salient features of the sequences in the SE Province may be summarized as follows:

i. The sub-*plenus* erosion surface can be traced over the whole of south-east England. It is overlain by an almost uniform succession of marls and chalks (Beds 1–8).

ii. The mid-Cenomanian non-sequence is shown to be a very significant horizon, at which there is evidence of a pause in sedimentation, warping and erosion.

iii. The Zone 9/Zone 10 non-sequence represents a widespread break in the succession, although on a smaller scale than the mid-Cenomanian non-sequence.

iv. The Albian/Cenomanian boundary is a complex junction which is almost transitional in some places but represents a marked hiatus at others.

v. The Chert Beds contain no dateable elements, are overlain by Cenomanian sands and chalks, and underlain by greensands which contain *Stoliczkaia dispar* faunas in the derived condition.

b. South-west Province

This includes the mid-Cretaceous of the counties of Dorset and Devon, and a small area of southernmost Somerset. The successions have been the subject of much controversy in recent years (see discussion of Kennedy 1969). The dominant lithology in the area is that of the Upper Greensand, which presents problems in itself. Fossils of any kind are rare, and those that are found are generally long-ranging species of little stratigraphic value. The major micropalaeontological problem is the collection of fresh material. Most sections of the Upper Greensand are decalcified to some depth, and when fresh material is found it usually proves too hard for satisfactory processing. Acid must be used and the micropalaeontologist has to rely on the glauconitic casts and mineral infillings of foraminifera which have to be identified by comparison with normally preserved material. In the Haldon Hills, however, silicified foraminifera and ostracods have been brushed from the outer surfaces of some of the cherts, and some idea of the microfauna has been obtained. These factors preclude comprehensive micropalaeontological analysis of samples from the area and gaps in our knowledge still remain.

The SW Province is bordered to the east by the Mid-Dorset Swell and to the south-west by the margin of the Cenomanian sea. As it is fairly well defined it is appropriate to begin with a discussion of the eastern margin, running from Buckland Newton towards Swanage.

1. *The Mid-Dorset Swell; the Chalk and the Basement Bed*

The succession at Buckland Newton, shown in Fig. 21, p. 76, is of Upper Greensand, with its phosphatized *S. dispar* Zone fauna, overlain by some 25–30 m of Lower Chalk. The Chalk succession belongs in Zone 13, with only its lowest levels containing a fauna more akin to that of Zone 12. The phosphate Basement Bed yields elements of Lower Cenomanian faunas as well as the

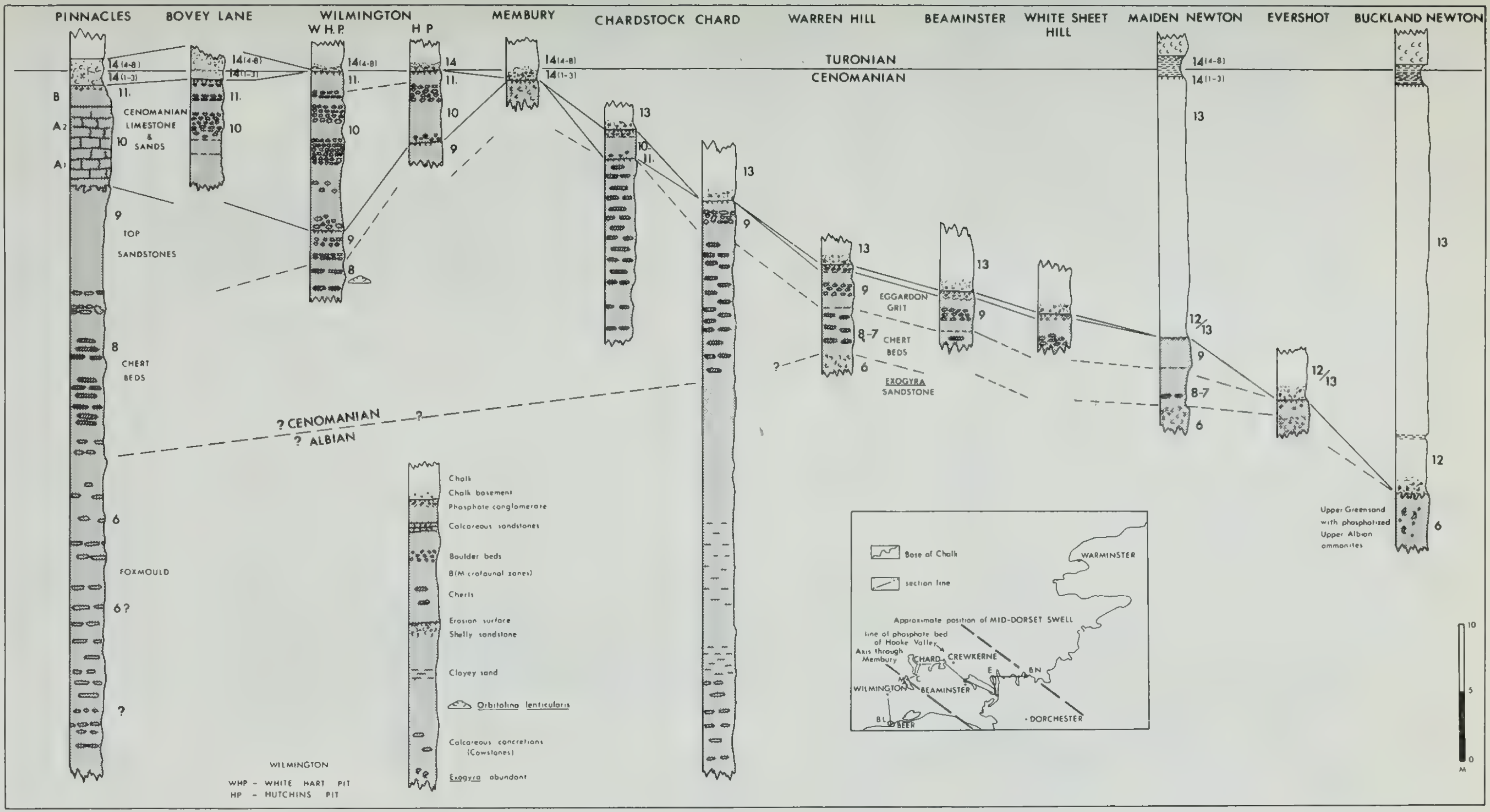

PINNACLES
BOVEY LANE
WILMINGTON
W.H.P.
H P
MEMBURY
CHARDSTOCK
CHARD
WARREN HILL
BEAMINSTER
WHITE SHEET HILL
MAIDEN NEWTON
EVERSHOT
BUCKLAND NEWTON
TURONIAN
CENOMANIAN
14(4-8)
14(1-3)
11.
10
9
8
8-7
6
6?
12/13
12
13
B
A2
A1
CENOMANIAN LIMESTONE & SANDS
TOP SANDSTONES
CHERT BEDS
FOXMOULD
EGGARDON GRIT
EXOGYRA SANDSTONE
? CENOMANIAN
? ALBIAN
Upper Greensand with phosphatized Upper Albian ammonites
Chalk
Chalk basement
Phosphate conglomerate
Calcareous sandstones
Boulder beds
B(M.crofaunal zones)
Cherts
Erosion surface
Shelly sandstone
Clayey sand
Orbitolina lenticularis
Calcareous concretions (Cowstones)
Exogyra abundant
WILMINGTON
WHP - WHITE HART PIT
HP - HUTCHINS PIT
Base of Chalk
section line
Approximate position of MID-DORSET SWELL
line of phosphate bed of Hooke Valley
Axis through Membury
WARMINSTER
CHARD
CREWKERNE
BEAMINSTER
WILMINGTON
BEER
BL
M
C
E
BN
DORCHESTER
10
5
0
M

Fig. 28 A correlation of the mid-Cretaceous between central Dorset (Buckland Newton) and the south-east Devon coast.

more important Middle Cenomanian (*Turrilites costatus* assemblage) fauna. This complete admixture of Lower and Middle Cenomanian faunas, combined in an uppermost Middle Cenomanian matrix, indicates the importance of the mid-Cenomanian non-sequence at this locality.

Over the whole of the area, exposures in the mass of the Lower Chalk are rare, while those of the Chalk Basement Bed are relatively abundant. This is due to the marked break in slope at the junction of the chalk and greensand, which, over the greater part of Dorset, is produced by the hardness of the uppermost bed of the Upper Greensand – the Eggardon Grit – which tends to form a prominent ledge. Although the Basement Bed varies in age across the region previous workers have made very little use of this fact. Kennedy (1970) recognized that it became generally younger westwards, but his diagram (1970: fig. 19) disregards the distribution of his localities. When studied systematically an overall pattern emerges. The main trends are shown in Fig. 27. Drummond (1970: fig. 10) attempted to demonstrate a relationship between these sedimentological trends and underlying structures, and although no direct relationship between these structures and Lower and Middle Cenomanian depositional patterns is yet established, one is suspected. There are indications of a very slight trough (?) (Fig. 28) in the vicinity of Maiden Newton and the Hooke Valley. This can be followed through Evershot, ST 578050 (Fig. 29), where the Chalk Basement Bed includes a phosphatized *Turrilites acutus* assemblage fauna, to Standers Mill Plantation, SY 587976 (Fig. 30), marking the beginning of the rapid reduction in thickness of the Lower Chalk which continues as far as Chard and Chardstock. Between Standers Mill Plantation, White Sheet Hill, ST 493025 (Fig. 31), Horn Hill, Beaminster, ST 470032

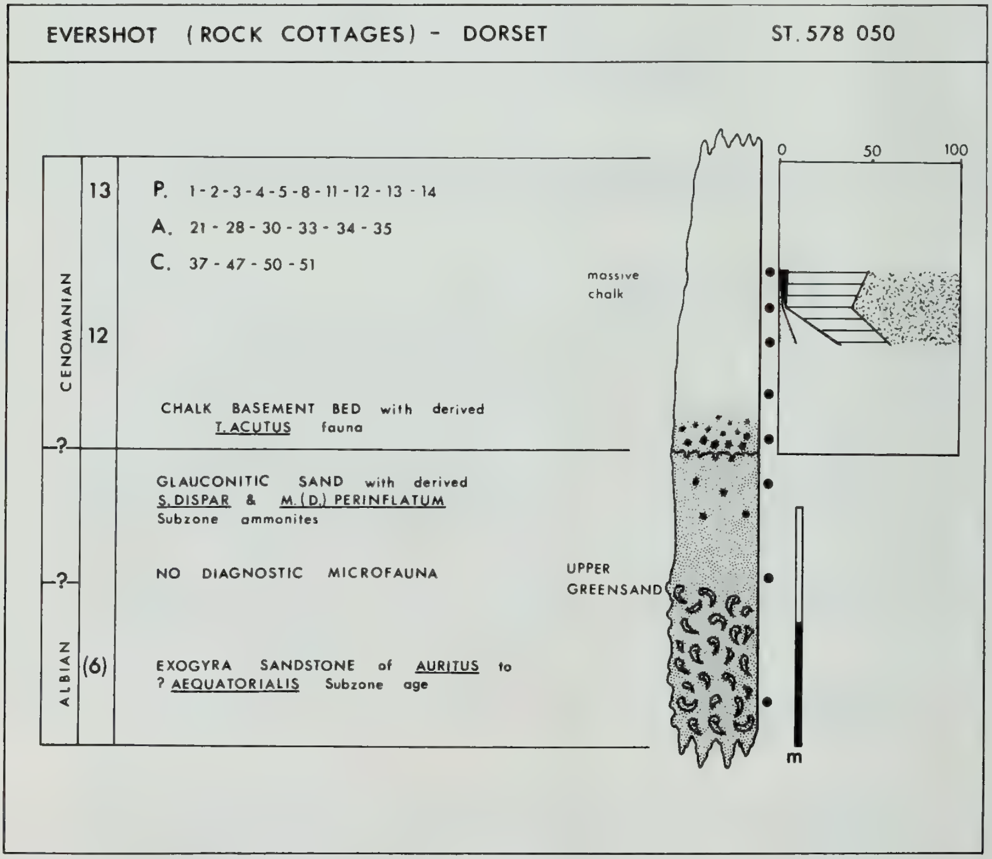

EVERSHOT (ROCK COTTAGES) - DORSET
ST. 578 050
CENOMANIAN
ALBIAN
13
12
(6)
?
?
P. 1-2-3-4-5-8-11-12-13-14
A. 21-28-30-33-34-35
C. 37-47-50-51
CHALK BASEMENT BED with derived T. ACUTUS fauna
GLAUCONITIC SAND with derived S. DISPAR & M. (D.) PERINFLATUM Subzone ammonites
NO DIAGNOSTIC MICROFAUNA
EXOGYRA SANDSTONE of AURITUS to ? AEQUATORIALIS Subzone age
massive chalk
UPPER GREENSAND
0
50
100
m

Fig. 29 Microfaunal details, Evershot, Dorset. The ornament used in the planktonic/benthonic ratio graph is explained on Fig. 12c. See Fig. 20 for explanation of letter code.

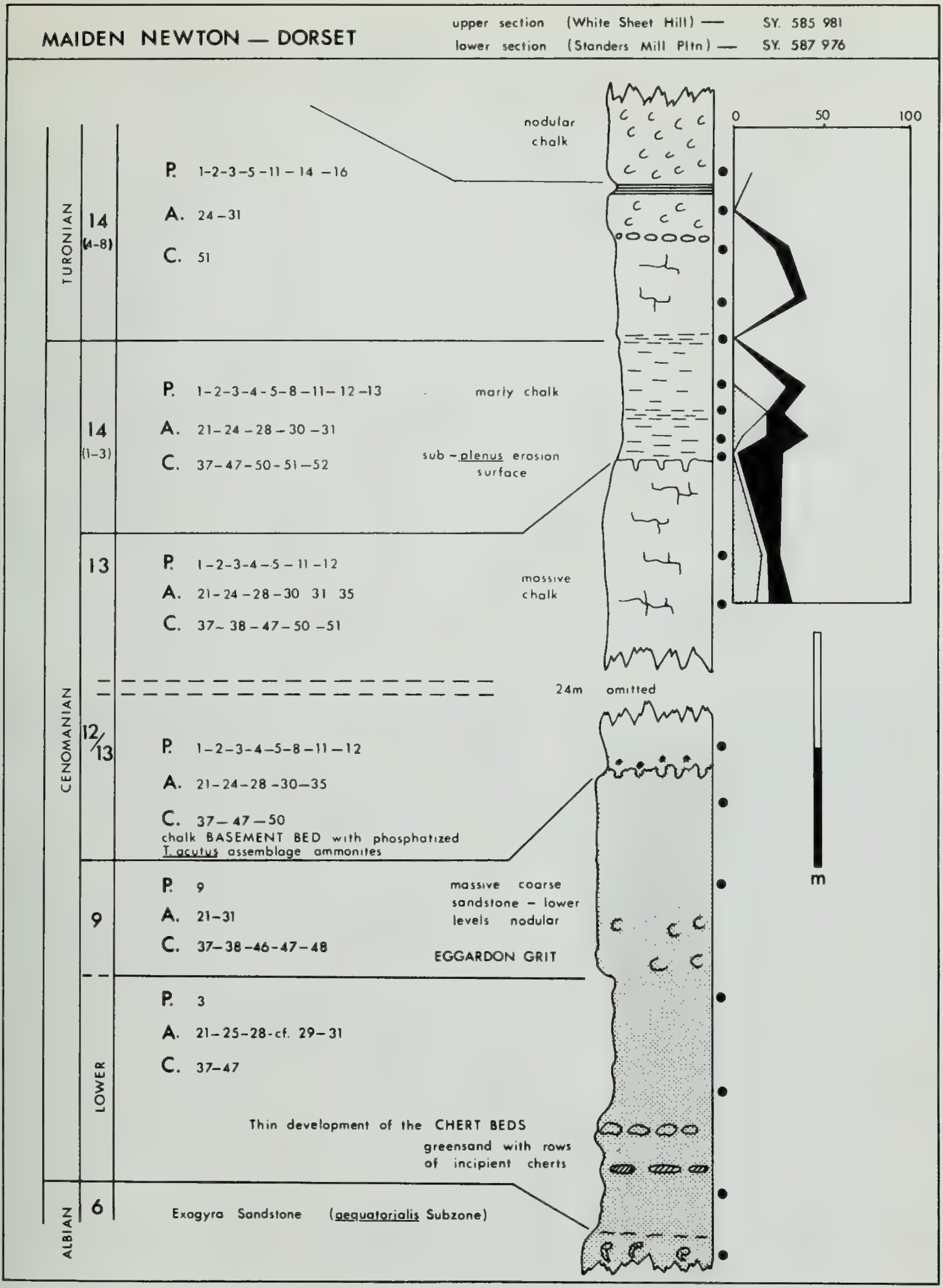

MAIDEN NEWTON — DORSET
upper section (White Sheet Hill) — SY. 585 981
lower section (Standers Mill Pltn) — SY. 587 976
TURONIAN
14
(4-8)
P. 1-2-3-5-11-14-16
A. 24-31
C. 51
nodular chalk
0
50
100
CENOMANIAN
14
(1-3)
P. 1-2-3-4-5-8-11-12-13
A. 21-24-28-30-31
C. 37-47-50-51-52
marly chalk
sub-plenus erosion surface
13
P. 1-2-3-4-5-11-12
A. 21-24-28-30 31 35
C. 37-38-47-50-51
massive chalk
24m omitted
12/13
P. 1-2-3-4-5-8-11-12
A. 21-24-28-30-35
C. 37-47-50
chalk BASEMENT BED with phosphatized T. acutus assemblage ammonites
9
P. 9
A. 21-31
C. 37-38-46-47-48
massive coarse sandstone - lower levels nodular
EGGARDON GRIT
m
LOWER
P. 3
A. 21-25-28-cf. 29-31
C. 37-47
Thin development of the CHERT BEDS
greensand with rows of incipient cherts
ALBIAN
6
Exogyra Sandstone (aequatorialis Subzone)

Fig. 30 Microfaunal details, Maiden Newton, Dorset. The ornament used in the planktonic/ benthonic ratio graphs is explained in Fig. 12b. See Fig. 20 for key to letter code.

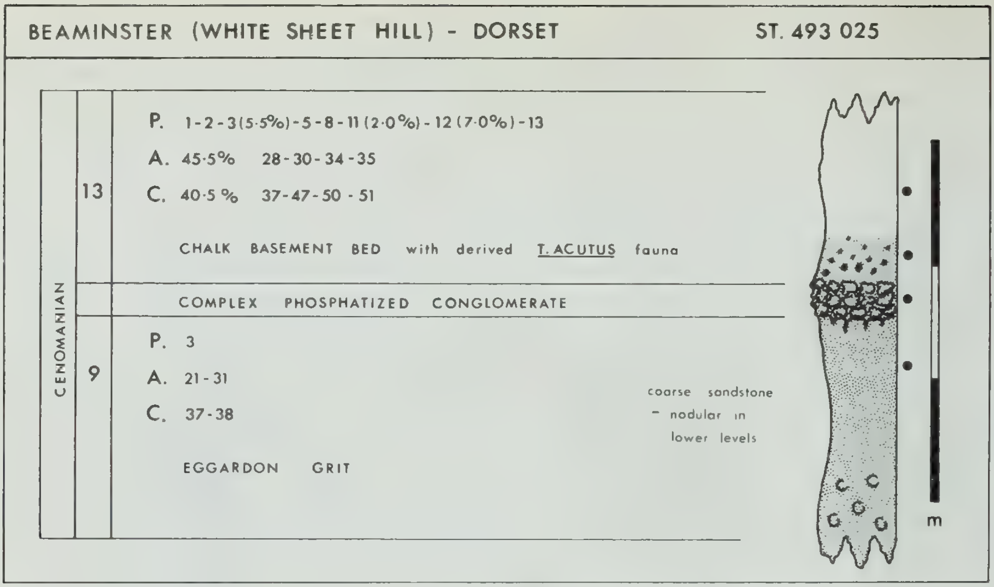

BEAMINSTER (WHITE SHEET HILL) - DORSET
ST. 493 025
CENOMANIAN
13
P. 1-2-3(5·5%)-5-8-11(2·0%)-12(7·0%)-13
A. 45·5% 28-30-34-35
C. 40·5% 37-47-50-51
CHALK BASEMENT BED with derived T. ACUTUS fauna
COMPLEX PHOSPHATIZED CONGLOMERATE
9
P. 3
A. 21-31
C. 37-38
EGGARDON GRIT
coarse sandstone
– nodular in
lower levels
m

Fig. 31 Microfaunal details, White Sheet Hill, Beaminster, Dorset. See Fig. 20 for key to letter code.

(Fig. 32), and Warren Hill, Crewkerne, ST 404103 (Fig. 33), a complex, phosphatized conglomerate is present below the Chalk Basement Bed. From Warren Hill to the most westerly locality of this traverse is little more than 16 km, but there are three more sections in the area important to our understanding of the stratigraphy. These are at Snowdon Hill, Chard, ST 313089 (Fig. 34), Storridge Hill, Chardstock, ST 316044 (Fig. 35), and Membury, ST 276042 (Fig. 36). Membury is particularly important since the fauna of the old disused quarry section is very well known. While faunal data is available for all the exposures mentioned above, too thin a section is present to permit a determination of the exact position of the Basement Bed within Zone 13. At Membury the Basement Bed is overlain by glauconitic chalk, which in turn is succeeded by approximately 15 m of white, splintery chalk (Fig. 36). The complex ammonite faunas from this sequence have been discussed by Kennedy (1970), who claimed that both Lower and Middle Cenomanian faunas are represented in the Basement Bed. He placed the unphosphatized fauna of the glauconitic matrix in the Upper Cenomanian and we accept this suggestion. The white, splintery chalk contains a microfauna remarkably similar to that of the Frétevou Chalk of the type Turonian, as described by Butt (1966), although the macrofauna, other than *Inoceramus* sp., is particularly sparse. The base of the glauconitic chalk belongs in the lower levels of the Plenus Marls (Beds 1–3), but even though Bed 4 can be faunally recognized the full thickness of Zone 14 is indeterminable because of the overgrown nature of the quarry.

The Membury succession indicates that in this area deposition above the mid-Cenomanian non-sequence began with the Plenus Marls, thus accounting for the great variety of ammonites in the Basement Bed. The sequence indicated by the microfauna is almost identical to that recorded from Bettrechies (northern France) by Robaszynski (1971). The area south-west of a line drawn south-eastwards from Membury (Fig. 27) shows the Cenomanian Limestones, which include as their uppermost member Bed C, the marginal equivalent of the Plenus Marls. The relationship of Bed C to the Plenus Marls can be demonstrated at the Pinnacles, SY 220879 (Fig. 37), and the Bovey Lane Sandpit, SY 217900 (Fig. 38). These localities are discussed later.

The more southerly traverse along the Dorset coast westwards from Swanage is shown in Fig. 39. The Lower Chalk of this coastline is relatively straightforward, and is commonly reduced to a thickness of a few metres by intense Tertiary shearing. At Lulworth Cove and Durdle Door the Basement Bed can be dated adequately (Zones 11(ii) and 12 respectively) and the pattern of the more northerly traverse is repeated. Eggardon Hill, SY 540950 (Fig. 40), and Askerswell, SY 529923, are the most westerly localities at which the Lower Chalk can be seen on this traverse, and in the latter its thickness is between 8 and 12 m. The next Cenomanian locality in a westerly direction is at Humble Point where the Cenomanian Limestone occupies this interval.

It is concluded that the Lower Chalk succession above the mid-Cenomanian non-sequence was deposited by a transgression over the eroded surface of the Lower and Middle Cenomanian, and all the determinable sedimentation trends appear to be subparallel to the edge of the Mid-Dorset Swell; see Fig. 27.

(cont. p. 98)

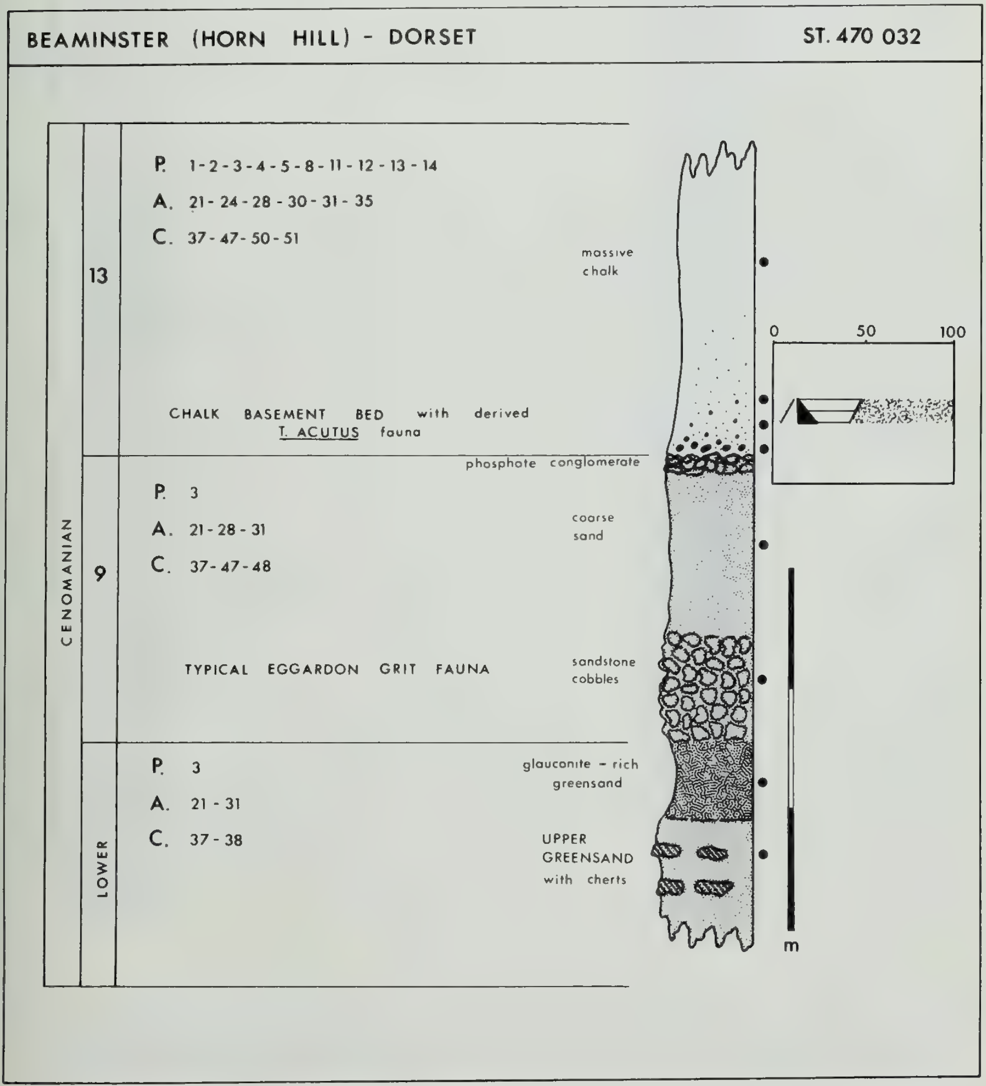

BEAMINSTER (HORN HILL) - DORSET
ST. 470 032
CENOMANIAN
13
P. 1-2-3-4-5-8-11-12-13-14
A. 21-24-28-30-31-35
C. 37-47-50-51
massive chalk
CHALK BASEMENT BED with derived T. ACUTUS fauna
phosphate conglomerate
9
P. 3
A. 21-28-31
C. 37-47-48
coarse sand
TYPICAL EGGARDON GRIT FAUNA
sandstone cobbles
LOWER
P. 3
A. 21-31
C. 37-38
glauconite - rich greensand
UPPER GREENSAND with cherts
0
50
100
m

Fig. 32 Microfaunal details, Horn Hill, Beaminster, Dorset. The ornament used in the planktonic/benthonic ratio graph is explained on Fig. 12c. See Fig. 20 for key to letter code.

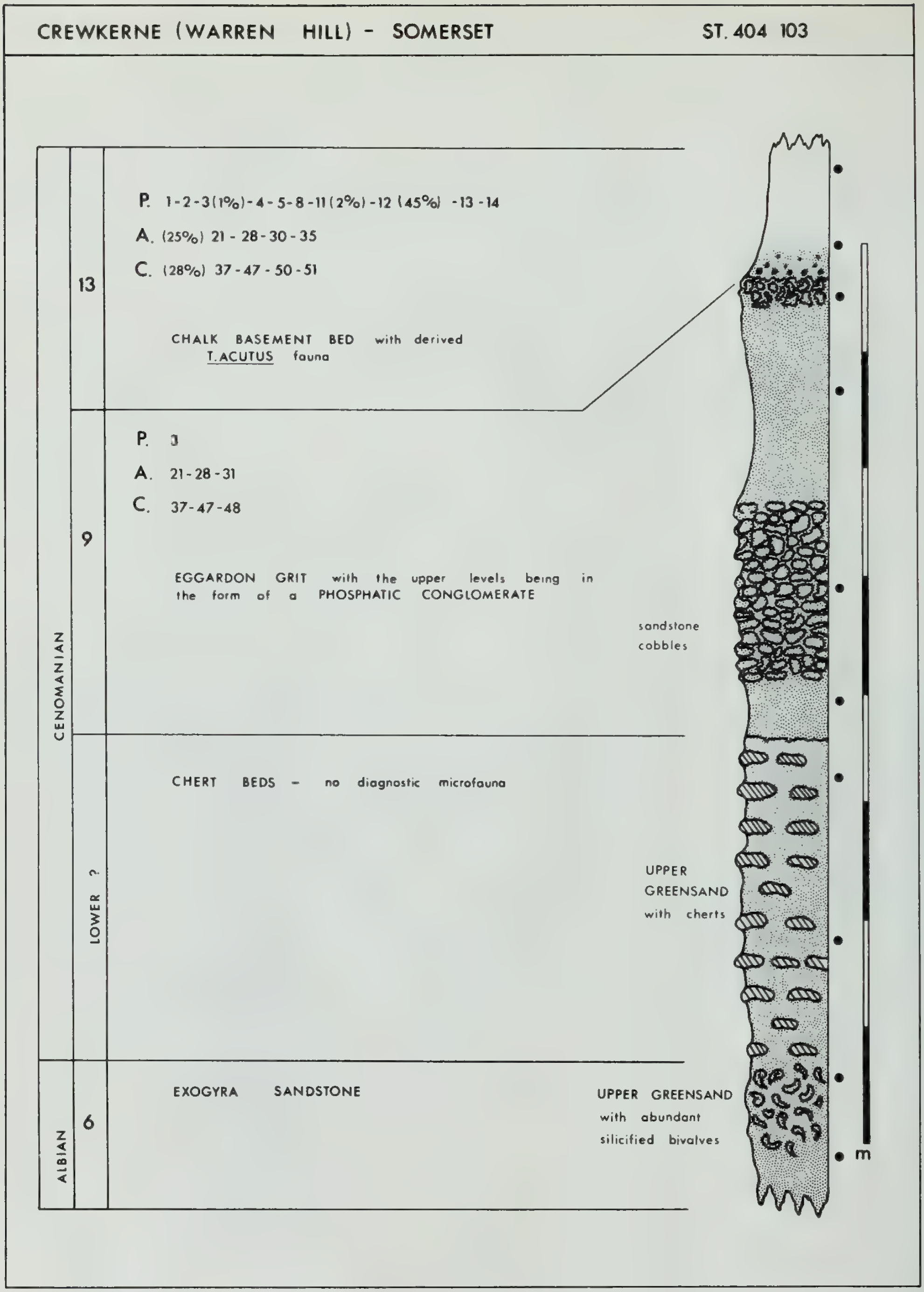

CREWKERNE (WARREN HILL) - SOMERSET
ST. 404 103
13
P. 1-2-3(1%)-4-5-8-11(2%)-12 (45%) -13-14
A. (25%) 21-28-30-35
C. (28%) 37-47-50-51
CHALK BASEMENT BED with derived T. ACUTUS fauna
9
P. 3
A. 21-28-31
C. 37-47-48
EGGARDON GRIT with the upper levels being in the form of a PHOSPHATIC CONGLOMERATE
sandstone cobbles
CENOMANIAN
LOWER ?
CHERT BEDS - no diagnostic microfauna
UPPER GREENSAND with cherts
ALBIAN
6
EXOGYRA SANDSTONE
UPPER GREENSAND with abundant silicified bivalves
m

Fig. 33 Microfaunal details, Warren Hill, Crewkerne, Somerset. See Fig. 20 for key to letter code.

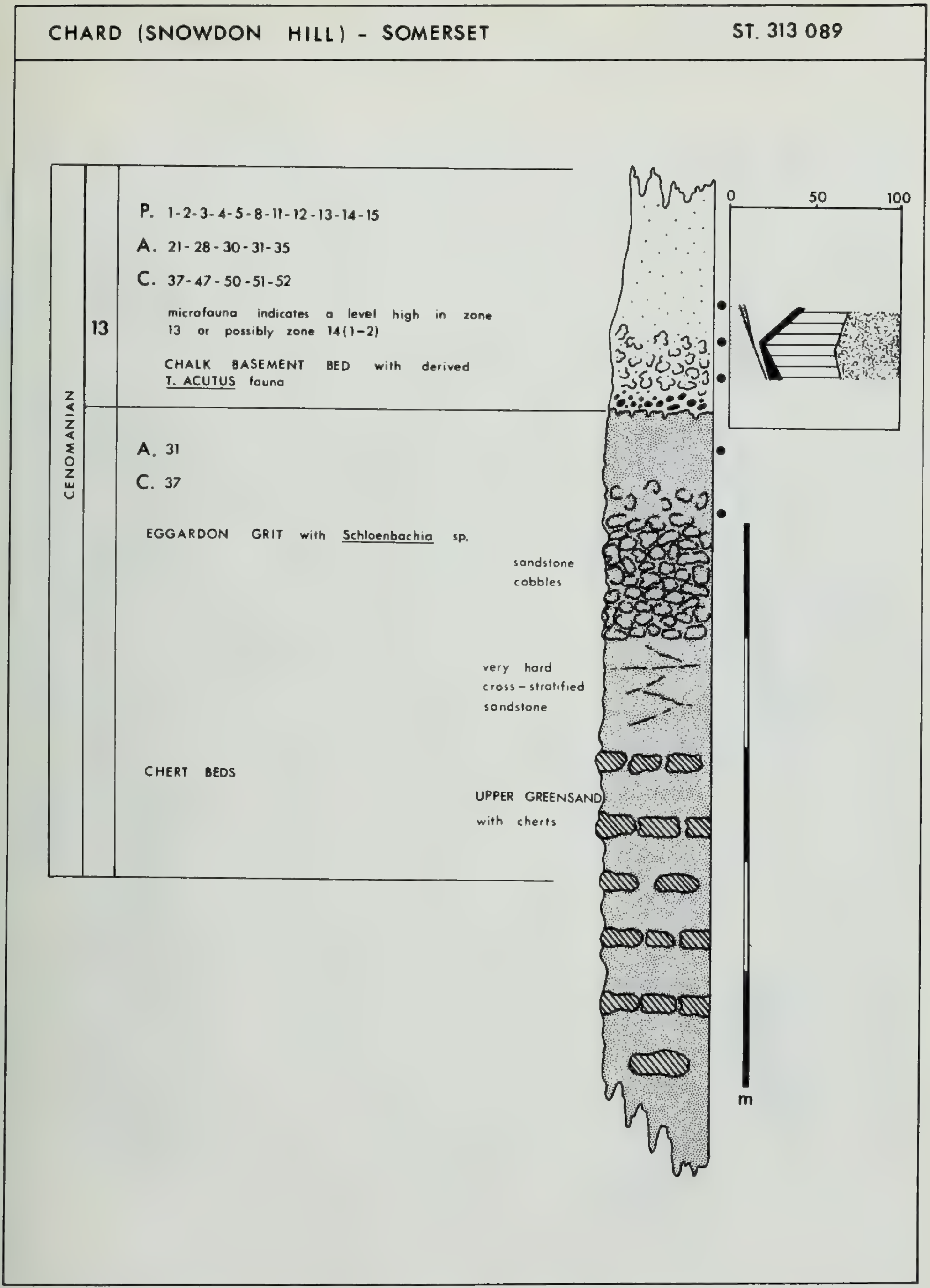

CHARD (SNOWDON HILL) - SOMERSET
ST. 313 089
CENOMANIAN
13
P. 1-2-3-4-5-8-11-12-13-14-15
A. 21-28-30-31-35
C. 37-47-50-51-52
microfauna indicates a level high in zone 13 or possibly zone 14(1-2)
CHALK BASEMENT BED with derived T. ACUTUS fauna
A. 31
C. 37
EGGARDON GRIT with Schloenbachia sp.
sandstone cobbles
very hard cross-stratified sandstone
CHERT BEDS
UPPER GREENSAND with cherts
0
50
100
m

Fig. 34 Microfaunal details, Snowdon Hill, Chard, Somerset. The ornament used in the planktonic/benthonic ratio graph is explained in Fig. 12c. See Fig. 20 for key to letter code.

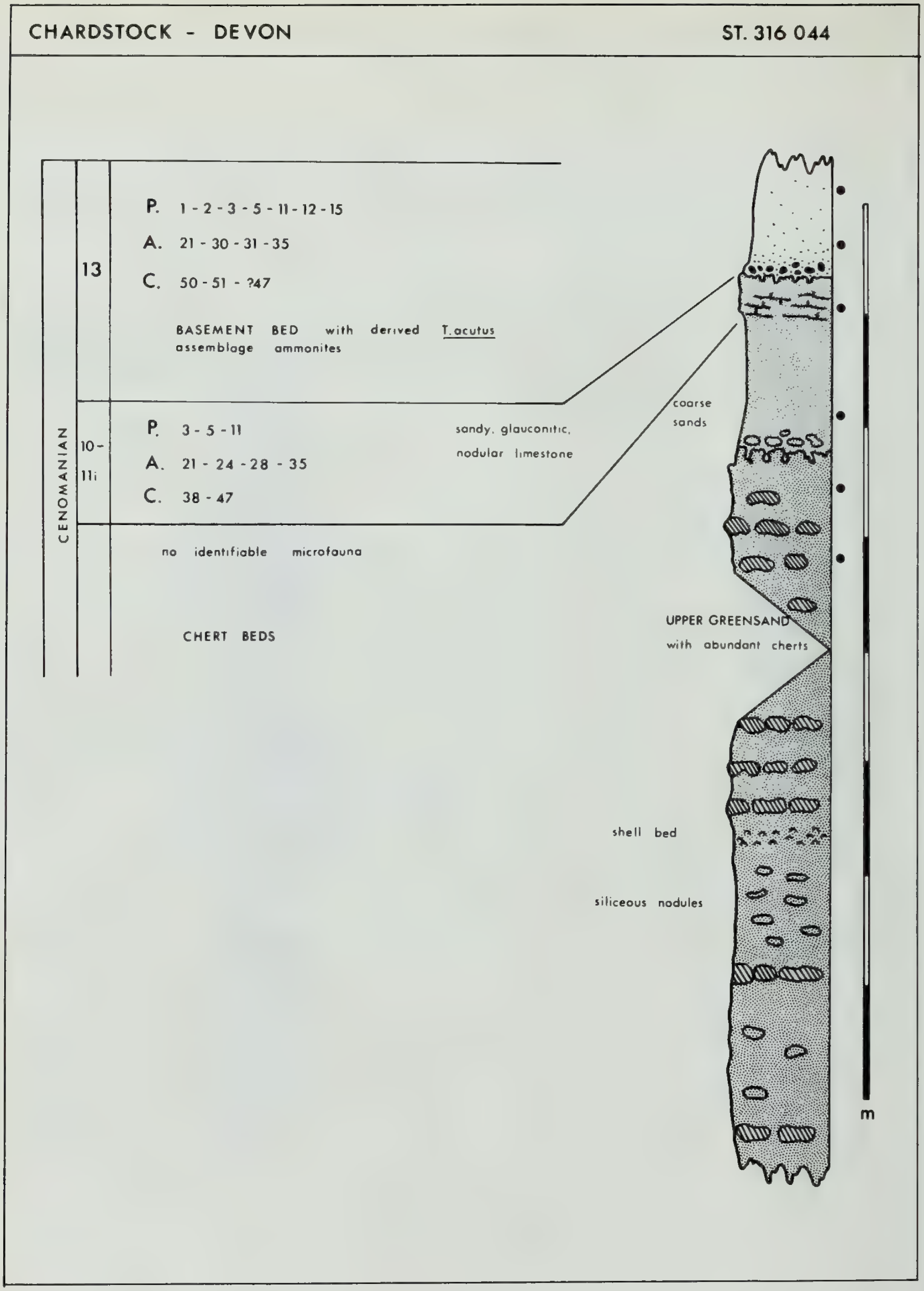

CHARDSTOCK - DEVON
ST. 316 044
CENOMANIAN
13
P. 1 - 2 - 3 - 5 - 11 - 12 - 15
A. 21 - 30 - 31 - 35
C. 50 - 51 - ?47
BASEMENT BED with derived T. acutus assemblage ammonites
10-11i
P. 3 - 5 - 11
A. 21 - 24 - 28 - 35
C. 38 - 47
sandy, glauconitic, nodular limestone
coarse sands
no identifiable microfauna
CHERT BEDS
UPPER GREENSAND with abundant cherts
shell bed
siliceous nodules
m

Fig. 35 Microfaunal details, Storridge Hill, Chardstock, Devon. See Fig. 20 for key to letter code.

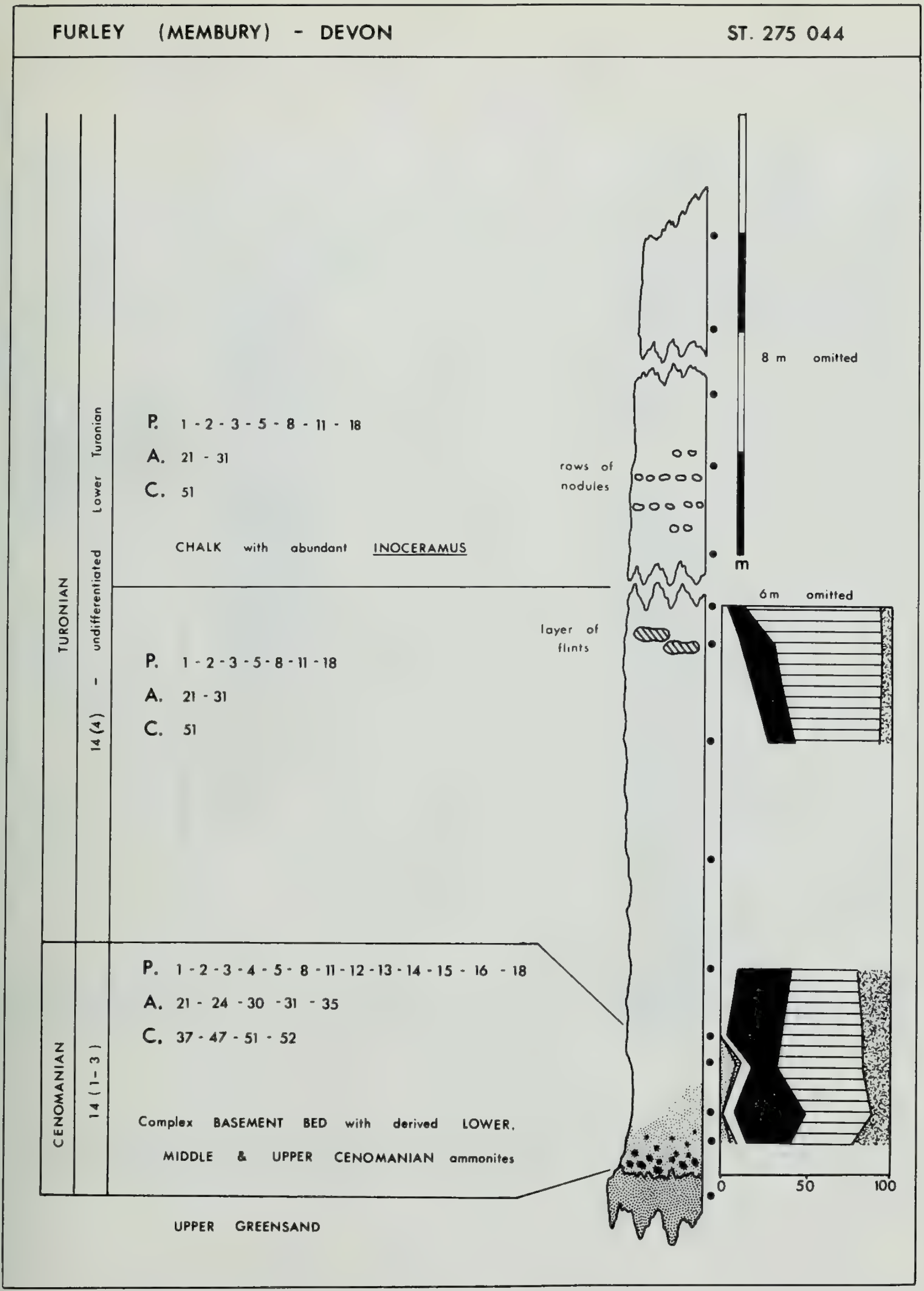

FURLEY (MEMBURY) - DEVON
ST. 275 044
TURONIAN
14 (4) - undifferentiated Lower Turonian
P. 1 - 2 - 3 - 5 - 8 - 11 - 18
A. 21 - 31
C. 51
CHALK with abundant INOCERAMUS
P. 1 - 2 - 3 - 5 - 8 - 11 - 18
A. 21 - 31
C. 51
CENOMANIAN
14 (1 - 3)
P. 1 - 2 - 3 - 4 - 5 - 8 - 11 - 12 - 13 - 14 - 15 - 16 - 18
A. 21 - 24 - 30 - 31 - 35
C. 37 - 47 - 51 - 52
Complex BASEMENT BED with derived LOWER, MIDDLE & UPPER CENOMANIAN ammonites
UPPER GREENSAND
rows of nodules
layer of flints
8 m omitted
m
6 m omitted
0
50
100

Fig. 36 Microfaunal details, Membury, Devon. The ornament used in the planktonic/benthonic ratio is explained in Fig. 12c. See Fig. 20 for key to letter code.

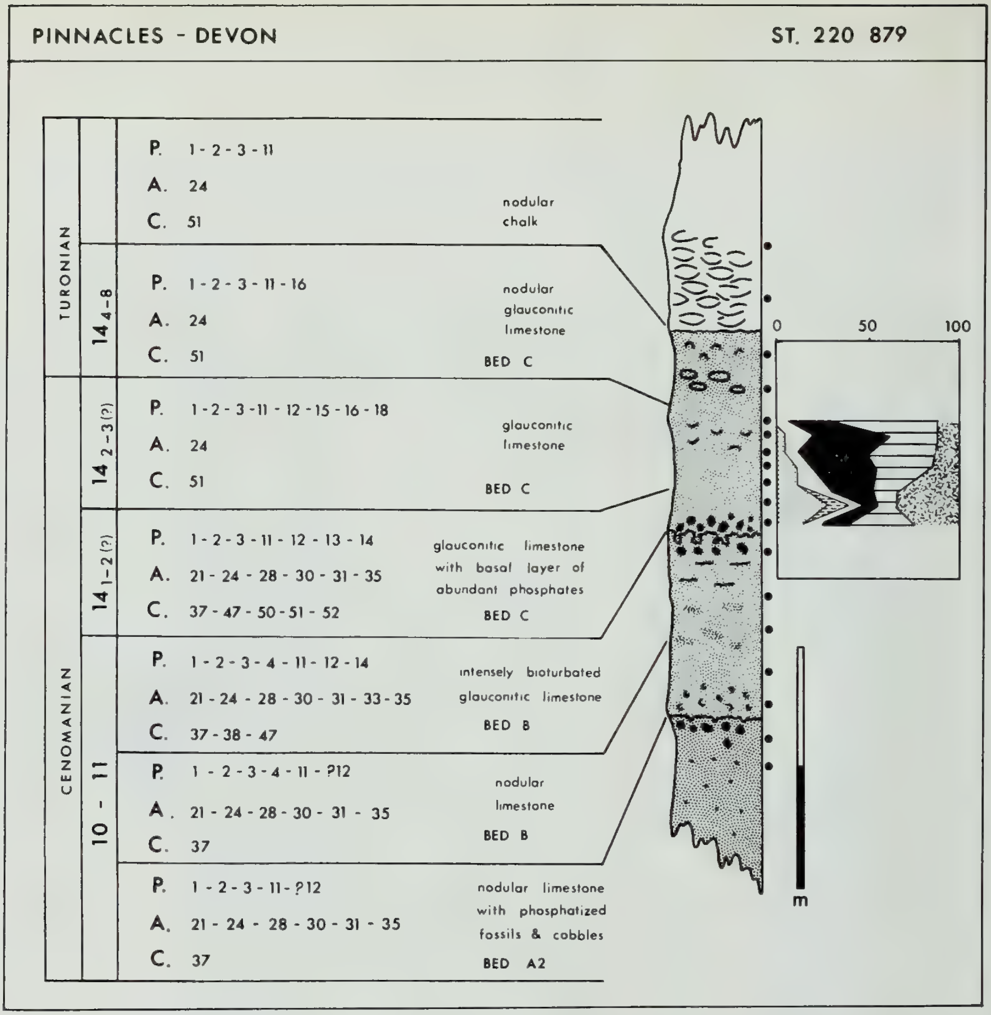

PINNACLES - DEVON
ST. 220 879
TURONIAN
CENOMANIAN
14 4-8
14 2-3(?)
14 1-2(?)
10 - 11
P. 1-2-3-11
A. 24
C. 51
nodular chalk
P. 1-2-3-11-16
A. 24
C. 51
nodular glauconitic limestone
BED C
P. 1-2-3-11-12-15-16-18
A. 24
C. 51
glauconitic limestone
BED C
P. 1-2-3-11-12-13-14
A. 21-24-28-30-31-35
C. 37-47-50-51-52
glauconitic limestone with basal layer of abundant phosphates
BED C
P. 1-2-3-4-11-12-14
A. 21-24-28-30-31-33-35
C. 37-38-47
intensely bioturbated glauconitic limestone
BED B
P. 1-2-3-4-11-?12
A. 21-24-28-30-31-35
C. 37
nodular limestone
BED B
P. 1-2-3-11-?12
A. 21-24-28-30-31-35
C. 37
nodular limestone with phosphatized fossils & cobbles
BED A2
0
50
100
m

Fig. 37 Microfaunal details, The Pinnacles, Little Beach, Branscombe, Devon. The ornament used in the planktonic/benthonic ratio graph is explained in Fig. 12c. See Fig. 20 for key to letter code.

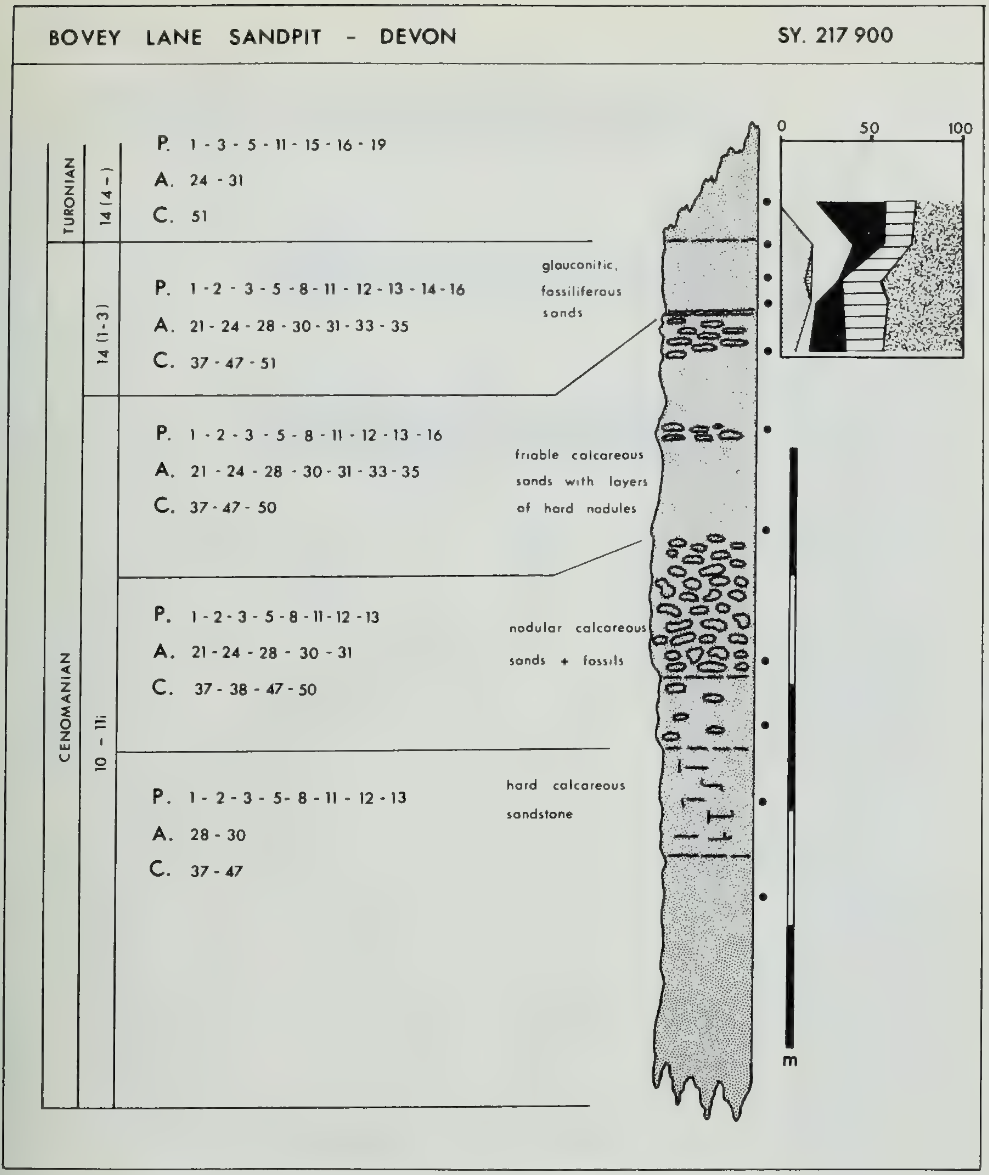

BOVEY LANE SANDPIT - DEVON
SY. 217 900
TURONIAN
14 (4 -)
P. 1 - 3 - 5 - 11 - 15 - 16 - 19
A. 24 - 31
C. 51
CENOMANIAN
14 (1-3)
P. 1 - 2 - 3 - 5 - 8 - 11 - 12 - 13 - 14 - 16
A. 21 - 24 - 28 - 30 - 31 - 33 - 35
C. 37 - 47 - 51
glauconitic, fossiliferous sands
10 - 11i
P. 1 - 2 - 3 - 5 - 8 - 11 - 12 - 13 - 16
A. 21 - 24 - 28 - 30 - 31 - 33 - 35
C. 37 - 47 - 50
friable calcareous sands with layers of hard nodules
P. 1 - 2 - 3 - 5 - 8 - 11 - 12 - 13
A. 21 - 24 - 28 - 30 - 31
C. 37 - 38 - 47 - 50
nodular calcareous sands + fossils
P. 1 - 2 - 3 - 5 - 8 - 11 - 12 - 13
A. 28 - 30
C. 37 - 47
hard calcareous sandstone
0
50
100
m

Fig. 38 Microfaunal details, Bovey Lane Sandpit, Beer, Devon. The ornament used in the planktonic-benthonic ratio graph is explained in Fig. 12c. See Fig. 20 for key to letter code.

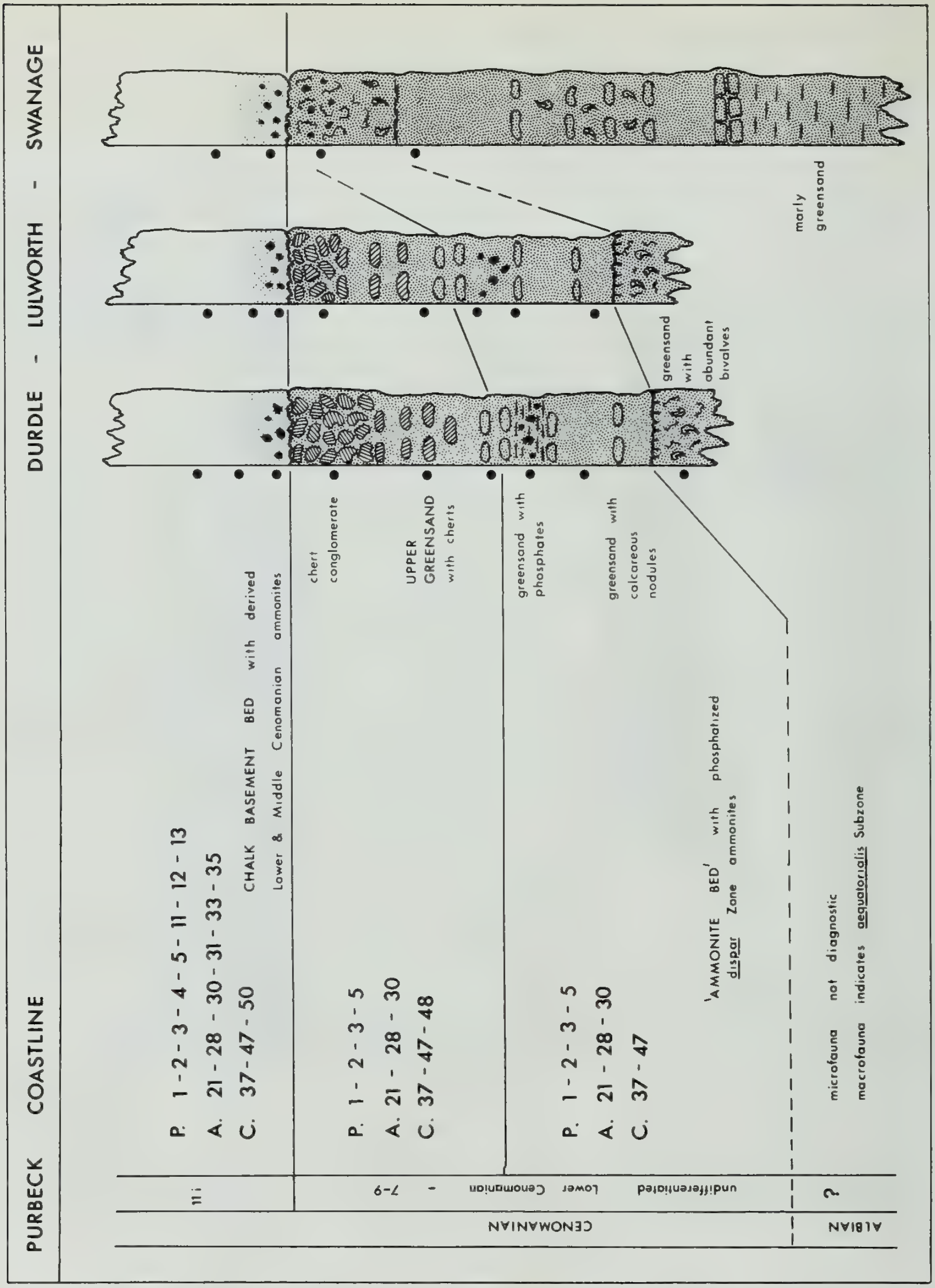

PURBECK COASTLINE
DURDLE - LULWORTH - SWANAGE
P. 1 - 2 - 3 - 4 - 5 - 11 - 12 - 13
A. 21 - 28 - 30 - 31 - 33 - 35
C. 37 - 47 - 50
CHALK BASEMENT BED with derived
Lower & Middle Cenomanian ammonites
chert conglomerate
UPPER GREENSAND with cherts
P. 1 - 2 - 3 - 5
A. 21 - 28 - 30
C. 37 - 47 - 48
greensand with phosphates
greensand with calcareous nodules
P. 1 - 2 - 3 - 5
A. 21 - 28 - 30
C. 37 - 47
'AMMONITE BED' with phosphatized
dispar Zone ammonites
greensand with abundant bivalves
marly greensand
microfauna not diagnostic
macrofauna indicates aequatorialis Subzone
11i
undifferentiated Lower Cenomanian - 7-9
CENOMANIAN
?
ALBIAN

Fig. 39 Microfaunal details, Purbeck coastline. See Fig. 20 for key to letter code.

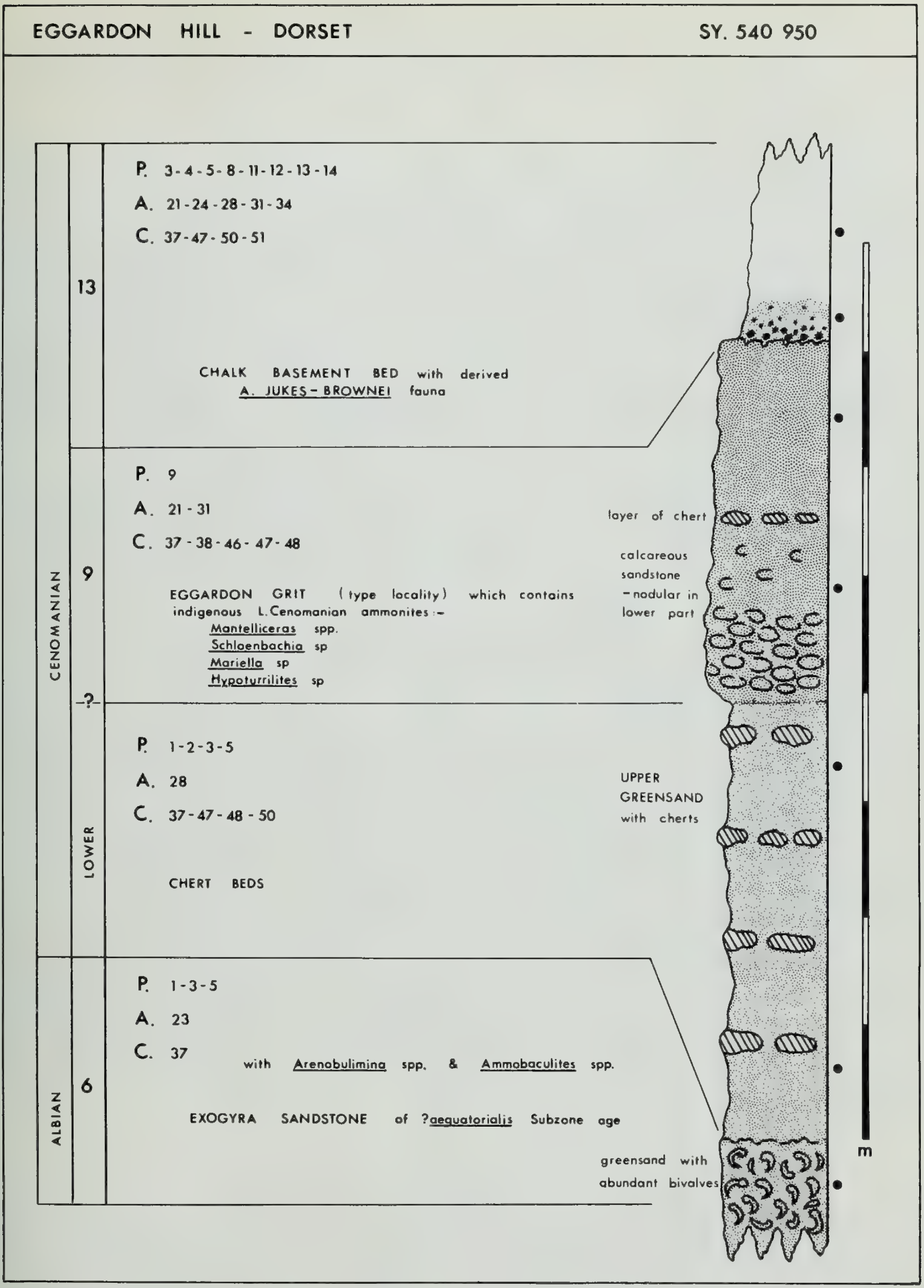

EGGARDON HILL - DORSET
SY. 540 950
CENOMANIAN
ALBIAN
LOWER
13
9
-?-
6
P. 3-4-5-8-11-12-13-14
A. 21-24-28-31-34
C. 37-47-50-51
CHALK BASEMENT BED with derived A. JUKES-BROWNEI fauna
P. 9
A. 21-31
C. 37-38-46-47-48
EGGARDON GRIT (type locality) which contains indigenous L.Cenomanian ammonites :-
Mantelliceras spp.
Schloenbachia sp
Mariella sp
Hypoturrilites sp
P. 1-2-3-5
A. 28
C. 37-47-48-50
CHERT BEDS
P. 1-3-5
A. 23
C. 37
with Arenobulimina spp. & Ammobaculites spp.
EXOGYRA SANDSTONE of ?aequatorialis Subzone age
layer of chert
calcareous sandstone -nodular in lower part
UPPER GREENSAND with cherts
greensand with abundant bivalves
m

Fig. 40 Microfaunal details, Eggardon Hill, Dorset. See Fig. 20 for key to letter code.

2. *The margin of the Mid-Dorset Swell* (*the Upper Greensand*)

The succession below the mid-Cenomanian non-sequence presents none of the essentially simple trends that characterize the overlying Lower Chalk. The grits, sands, and sands with cherts forming this succession display a complex series of relationships frequently complicated by the presence of erosion surfaces.

West of Buckland Newton, where the uppermost Upper Greensand contains a phosphatized *S. dispar* Zone fauna, changes occur which become more important as the Hooke Valley is approached. Only two exposures of any note occur between Buckland Newton and Standers Mill Plantation, the first being at Great Head, ST 624045, and the second at Evershot (Fig. 29). At Great Head an *S. dispar* Zone fauna, similar to that at Buckland Newton, was recorded by Wilson *et al.* (1958). Between Great Head and Evershot the *Exogyra* Sandstone appears. This is a very rough, glauconitic sandstone, full of silicified bivalves, and a very useful field marker horizon. It has yielded an unphosphatized specimen of *M.* (*Mortoniceras*) aff. *commune* Spath and has been recorded as of *auritus* or *aequatorialis* Subzone age (Kennedy 1970 : 630). The greensand above the *Exogyra* Sandstone at Evershot has yielded phosphatized *S. dispar* Zone ammonites, although specimens are rare. The changes initiated at Evershot are continued in the river bank exposure at Standers Mill Plantation (Fig. 30), where both the 'Chert Beds' and the Eggardon Grit appear in the succession. The Chert Beds, with only small incipient siliceous concretions, occur between the Eggardon Grit and the *Exogyra* Sandstone. The Eggardon Grit was initially described from Eggardon Hill by Wilson *et al.* (1958), although many earlier workers have called this distinctive horizon the 'Calcareous Sandstone'. It is usually a very hard, glauconite-free, calcareous sandstone which, at several localities, has yielded Lower Cenomanian ammonites. As no contradictory evidence is forthcoming, it is now accepted as being of Lower Cenomanian age – Zone 9 in the microfaunal succession. The sparse microfauna from the *Exogyra* Sandstone suggests that the Upper Albian dating is probably correct. Although the evidence is not conclusive, the sands, which include the cherts at Standers Mill Plantation, contain faunal elements indicating a Lower Cenomanian age. Along the line of the Hooke Valley the Chert Beds thicken only slightly, but when traced south-westwards they thicken markedly. An additional complication is introduced along the Hooke Valley, where a distinctive bed of phosphatized cobbles and fossils is found between the Eggardon Grit and the Chalk Basement Bed. The fauna of the phosphate conglomerate is entirely Lower Cenomanian. The majority of the ammonite species present are also recorded from the phosphate bed seen on the Isle of Wight (Fig. 25) at the Zone 9/Zone 10 boundary. The dating of the Eggardon Grit as Zone 9 is in accord with the ammonite distribution. The phosphatized conglomerate can be traced the whole length of the Hooke Valley and is last seen at Warren Hill. It represents a hiatus of some magnitude, covering Zones 10–12 of the Cenomanian. This hiatus is related not only to that of the Zone 9/Zone 10 boundary in the Isle of Wight, but also the base of the Chalk in the Mere area. The Popple Bed and the Rye Hill Sands (Warminster Greensand) are therefore lateral equivalents of the Eggardon Grit, although the exact relationship is difficult to determine. It is also relevant to note the distribution of *Orbitolina lenticularis* at this time, occurring in the Rye Hill Sands, the lower levels of the Eggardon Grit at Wilmington and in the cliffs at Dunscombe (south Devon). The significance of *O. lenticularis* will be discussed later.

3. *The South-western Shelf* (*Cenomanian Limestones*)

Westwards from Warren Hill the Cenomanian Limestones and Sands first appear in the succession. The mid-Cenomanian non-sequence beneath Bed C (the marginal equivalent of the Plenus Marls) represents a hiatus which began in the Cenomanian (between the *Turrilites costatus* and *T. acutus* Assemblage Subzones of Kennedy 1969), while the underlying Eggardon Grit has been assigned to the Lower Cenomanian Zone 9. The Cenomanian Sands and Limestones therefore cover the whole, or a part of, Zones 10–11(i). In terms of the ammonite successions this would approximately equate with the *Mantelliceras dixoni* and *T. costatus* Assemblage Subzones of south-east England. The faunas of these sands and limestones have been studied in the sections at Chardstock (Fig. 35), Hutchins Pit, Wilmington, ST 216003 (Fig. 41), White Hart Sandpit,

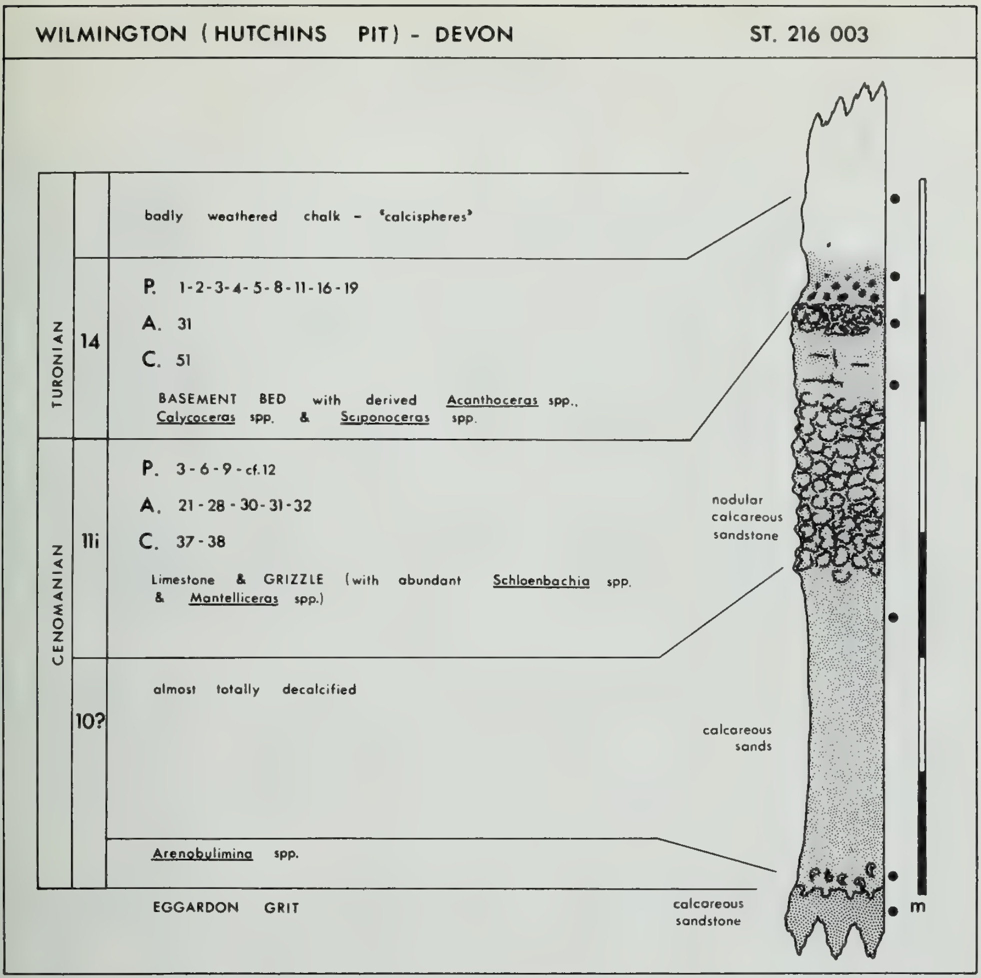

WILMINGTON (HUTCHINS PIT) - DEVON
ST. 216 003
TURONIAN
CENOMANIAN
14
11i
10?
badly weathered chalk - 'calcispheres'
P. 1-2-3-4-5-8-11-16-19
A. 31
C. 51
BASEMENT BED with derived Acanthoceras spp., Calycoceras spp. & Sciponoceras spp.
P. 3-6-9-cf.12
A. 21-28-30-31-32
C. 37-38
Limestone & GRIZZLE (with abundant Schloenbachia spp. & Mantelliceras spp.)
almost totally decalcified
Arenobulimina spp.
EGGARDON GRIT
nodular calcareous sandstone
calcareous sands
calcareous sandstone
m

Fig. 41 Microfaunal details, Hutchins Pit, Wilmington, Devon. See Fig. 20 for key to letter code.

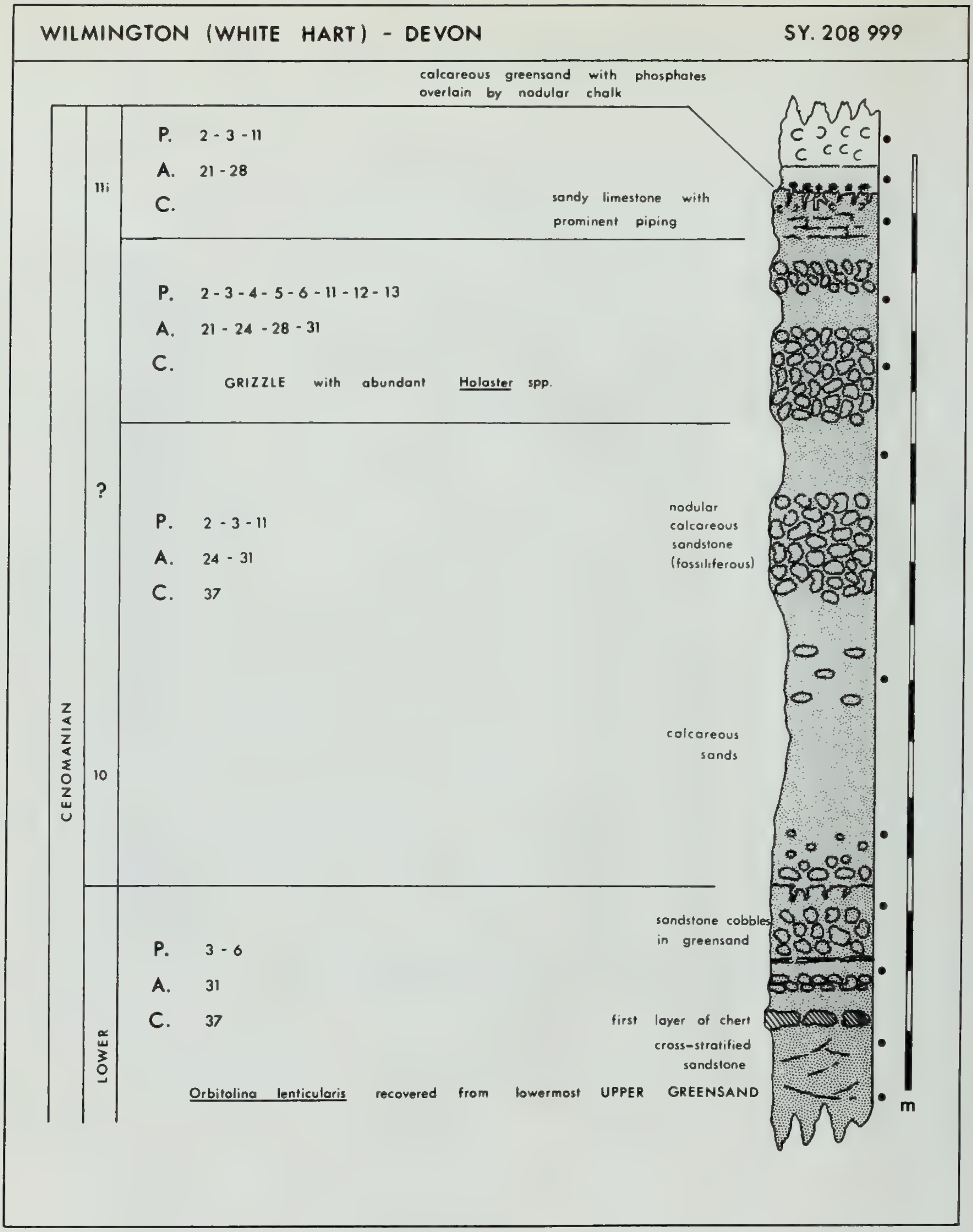

WILMINGTON (WHITE HART) - DEVON
SY. 208 999
calcareous greensand with phosphates overlain by nodular chalk
11i
P. 2 - 3 - 11
A. 21 - 28
C.
sandy limestone with prominent piping
P. 2 - 3 - 4 - 5 - 6 - 11 - 12 - 13
A. 21 - 24 - 28 - 31
C.
GRIZZLE with abundant Holaster spp.
?
P. 2 - 3 - 11
A. 24 - 31
C. 37
nodular calcareous sandstone (fossiliferous)
CENOMANIAN
10
calcareous sands
sandstone cobbles in greensand
LOWER
P. 3 - 6
A. 31
C. 37
first layer of chert
cross-stratified sandstone
Orbitolina lenticularis recovered from lowermost UPPER GREENSAND
m

Fig. 42 Microfaunal details, White Hart Sandpit, Wilmington, Devon. See Fig. 20 for key to letter code.

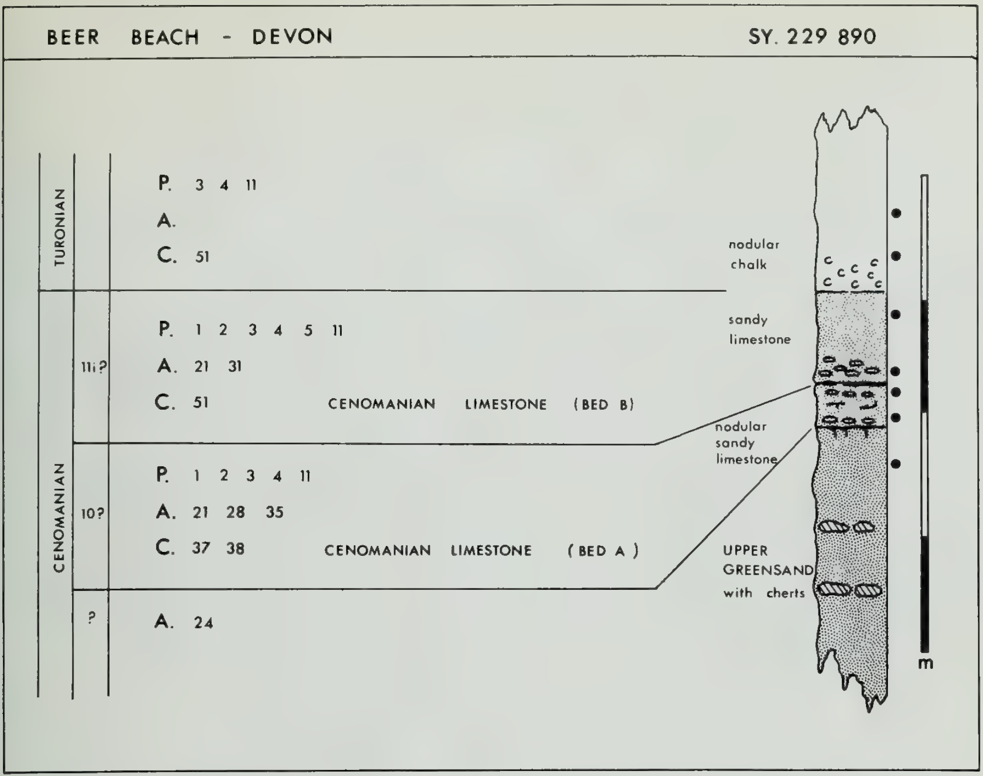

BEER BEACH - DEVON
SY. 229 890
TURONIAN
CENOMANIAN
11i?
10?
?
P. 3 4 11
A.
C. 51
P. 1 2 3 4 5 11
A. 21 31
C. 51
CENOMANIAN LIMESTONE (BED B)
P. 1 2 3 4 11
A. 21 28 35
C. 37 38
CENOMANIAN LIMESTONE (BED A)
A. 24
nodular chalk
sandy limestone
nodular sandy limestone
UPPER GREENSAND with cherts
m

Fig. 43 Microfaunal details, Beer Beach, Devon. See Fig. 20 for key to letter code.

Wilmington, SY 208999 (Fig. 42), the Pinnacles, Branscombe (Fig. 38), Beer Beach, SY 229890 (Fig. 43), and Bindon Cliff, SY 278897 (Fig. 44). The lithology and stratigraphy of these beds were described in detail by Smith (1957a, etc.) and Kennedy (1970) and only new evidence will be presented here. Although processing is very difficult, several of the zonally important species, including planktonic forms, have been recovered from most of the important sections. The faunas agree almost entirely with the predicted position between the Zone 9/Zone 10 and Zone 11(i)/Zone 11(ii) boundaries. The only feature of particular interest is the appearance of many planktonic forms – far more than would be expected at this level in the succession. Their occurrence will have to be considered in the light of regional studies of the palaeogeography. The presence of *Plectina cenomana*, *Arenobulimina advena*, *P. mariae*, *Gavelinella intermedia*, *G. baltica*, *G. cenomanica*, *Guembelitria harrisi*, *Hedbergella delrioensis*, *Praeglobotruncana stephani*, *H. washitensis*, and rare *Rotalipora cushmani* indicates a position in Zone 11(i). Although *P. cenomana* has not been recorded from Bed A1 or A2 of the Cenomanian Limestone succession (or from the sands at Wilmington) it cannot be assumed that this necessarily proves the presence of Zone 10 in the lower part of the succession. While it would be most satisfactory if this could be demonstrated, conclusive evidence is lacking. The ammonite faunas occur as rolled pebble-fossils and phosphatized casts and are not reliable. When inspected under short wave ultraviolet light these ammonites fluoresce bright yellow, indicating the presence of uranium, taken up with the phosphates which formed during exposure on the sea floor (Bromley 1965). The fauna of the lower limestone unit (Beds A1 and A2) is remarkably like that of the phosphate conglomerate of the Hooke Valley. This is not surprising as these two ammonite faunas accumulated during the same interval of geological time. Kennedy regarded this fauna as indicative of the *Mantelliceras saxbii* Assemblage Subzone of south-east England, although this age must refer to the faunal elements,

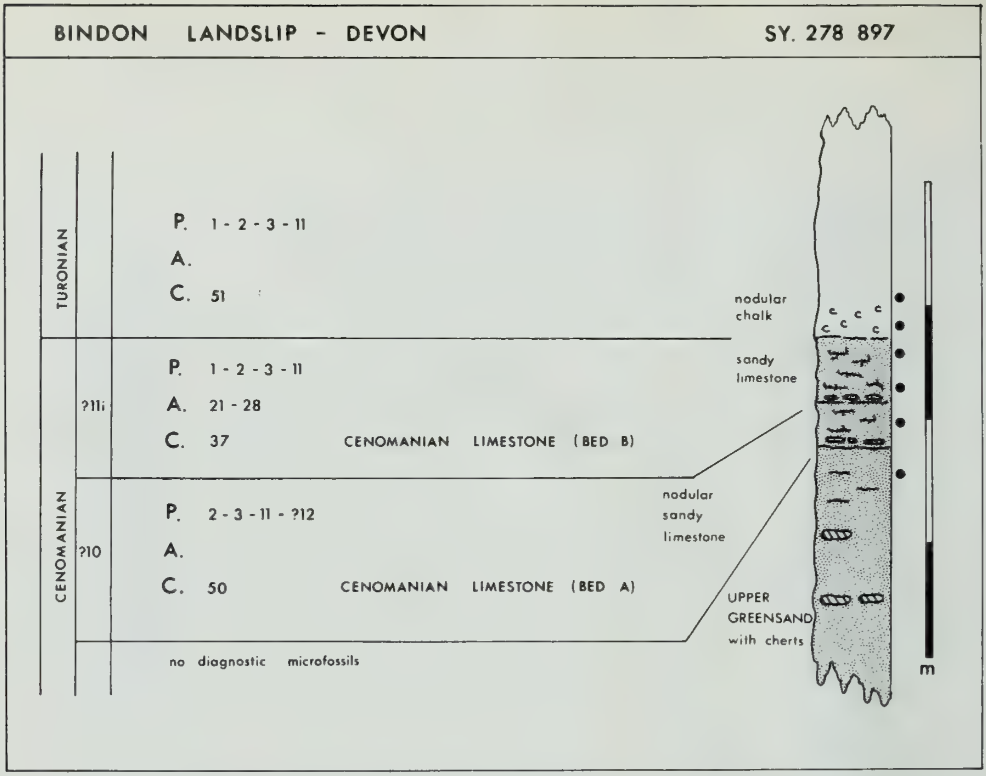

BINDON LANDSLIP - DEVON
SY. 278 897
TURONIAN
CENOMANIAN
?11i
?10
P. 1 - 2 - 3 - 11
A.
C. 51
P. 1 - 2 - 3 - 11
A. 21 - 28
C. 37
CENOMANIAN LIMESTONE (BED B)
P. 2 - 3 - 11 - ?12
A.
C. 50
CENOMANIAN LIMESTONE (BED A)
no diagnostic microfossils
nodular chalk
sandy limestone
nodular sandy limestone
UPPER GREENSAND with cherts
m

Fig. 44 Microfaunal details, Bindon Landslip, Devon. See Fig. 20 for key to letter code.

and not necessarily the enclosing sediment. The underlying Eggardon Grit (or Top Sandstones) is thought to belong to Zone 9 (? = *M. saxbii* Assemblage Subzone), and a derived *M. saxbii* assemblage fauna would be expected to occur in the overlying beds, which on the microfaunal content of the matrix are dated as Zone 10 (?). The upper limestone bed (Bed B) contains a poor ammonite fauna with elements from the *M. dixoni* assemblage. This derived fauna, together with the abundant *Holaster subglobosus* (Leske) encountered at this level, indicates a position in the Middle Cenomanian. This agrees with the Zone 11(i) dating of the microfauna. The microfauna is sparse but further work should add to the already extensive faunal lists.

The original suggestion of Hart (in discussion of Kennedy 1969) that the Cenomanian Limestones were of Upper Cenomanian age has, by further research, been shown to be incorrect. The warping and erosion below the Cenomanian Limestones, initially described by Smith (1957a, etc.) had been equated with the warping below the mid-Cenomanian non-sequence. This correlation was based on the abundance of planktonic microfauna in these sands and limestones. At that time the extent of the Zone 9/Zone 10 non-sequence was not fully appreciated and its effect beyond the Isle of Wight had not been considered. The determination of the trends which affect the beds below the mid-Cenomanian non-sequence proved beyond doubt that those of the flexures below the Cenomanian Limestones belonged to an earlier phase in the geological development of the area. The trends below the lower non-sequence determined by Smith are at a distinct angle to those immediately below the mid-Cenomanian break, and therefore cannot belong to the same suite. The interpretation put forward here differs from that given by other workers in this area in that the movements are ascribed to a level within the Lower Cenomanian and not immediately below the Albian/Cenomanian boundary.

4. *The South-western Shelf* (*the Upper Greensand*)

The succession below the mid-Cenomanian non-sequence exposed along the coast from Swanage to Branscombe (Devon) is closely similar to that in central Dorset. The lithological elements are almost identical, although there is some variation in their spatial relationships. The whole of the Upper Greensand will be dealt with, the uppermost levels being considered first. Sections on the Purbeck coast have been described in great detail by Wright (*in* Arkell 1947) and the included fauna is exceptionally well known. In central Dorset faunal evidence is sparse.

Wright (*in* Arkell 1947) demonstrates the presence of Albian *Hysteroceras orbignyi*, *H. varicosum*, *Callihoplites auritus* and *Mortoniceras aequatorialis* Subzones at various localities – all within the Upper Greensand succession. This faunal sequence is recorded below the *Exogyra* Sandstone and no indication is given of the age of this bed itself. Kennedy (1970 : 630) places it in the *aequatorialis* or *auritus* Subzones in central Dorset. This distinctive unit is remarkably constant both in appearance and subzonal position over a considerable part of central and southern Dorset. Its placing relative to the rest of the uppermost greensand succession of the Purbeck coast is shown in Fig. 45. However, the succession above the *Exogyra* Sandstone is more relevant. As at Standers Mill Plantation the Chert Beds appear above this level. On the coast the sands with cherts, which thicken rapidly westwards, are capped by a chert conglomerate, which immediately underlies the Chalk Basement Bed. The most important faunal horizon is the 'ammonite bed', traceable over a considerable length of coastline. The occurrence of this horizon led previous workers to record the *S. dispar* Zone in every section. It is interesting that the *Arrhaphoceras substuderi* Subzone has never been found at any locality. Wright (*in* Arkell 1947 : 184–185) lists the ammonite fauna and comments: '. . . and of these some are confined to Dorset, some are

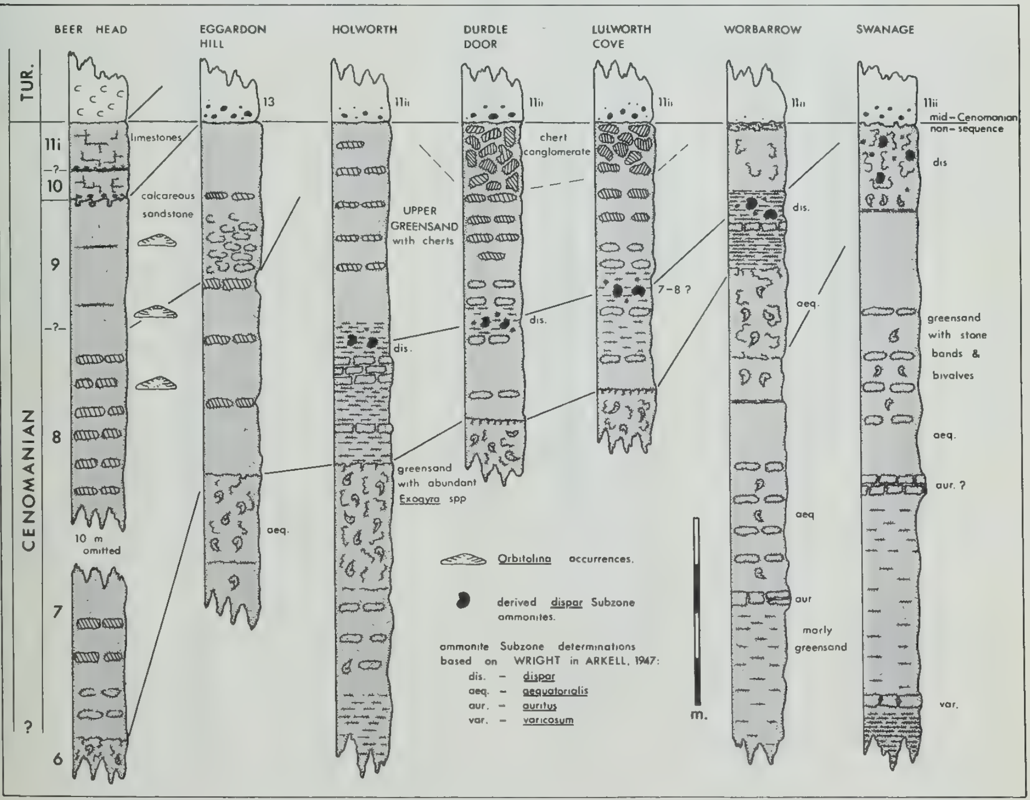

BEER HEAD
EGGARDON HILL
HOLWORTH
DURDLE DOOR
LULWORTH COVE
WORBARROW
SWANAGE
TUR.
CENOMANIAN
11i
–?–
10
9
–?–
8
7
?
6
10 m omitted
limestones
calcareous sandstone
13
11ii
chert conglomerate
UPPER GREENSAND with cherts
dis.
7–8 ?
aeq.
greensand with abundant Exogyra spp
mid – Cenomanian non – sequence
greensand with stone bands & bivalves
aur. ?
aeq
aur
marly greensand
var.
Orbitolina occurrences.
derived dispar Subzone ammonites.
ammonite Subzone determinations based on WRIGHT in ARKELL, 1947:
dis. – dispar
aeq. – aequatorialis
aur. – auritus
var. – varicosum
m.

Fig. 45 A correlation of the uppermost Upper Greensand of the Dorset-Devon coastline.

members of the semi-derived Cambridge Greensand fauna, and by their occurrence in Dorset can be placed stratigraphically.'

We have studied the relevant sections in detail and emphasize the following points, all of which suggest a different interpretation.

i. The ammonites found are all phosphatized.

ii. Most specimens of *Mortoniceras* sp. we found had been broken before phosphatization.

iii. The microfauna of the 'ammonite bed' includes *Marssonella trochus* (d'Orbigny), *Tritaxia pyramidata*, *Arenobulimina advena*, *Dorothia gradata* (Berthelin), *Gavelinella cenomanica*, *G. intermedia*, *Lingulogavelinella jarzevae*, *Heterohelix moremani*, *Guembelitria harrisi*, *Hedbergella delrioensis*, and *Praeglobotruncana stephani/P. delrioensis*, which indicates a horizon quite foreign to the Upper Albian. While some of the key species are absent there, the evidence suggests a position in the Lower Cenomanian (Zones 7–9).

Except that *Arenobulimina anglica*, *Marssonella ozawai* and *Flourensina intermedia* are missing the microfauna of the ammonite bed is almost identical with that described from the Cambridge Greensand. Although the value of the ammonite bed fauna is not clear cut it is suggestive of

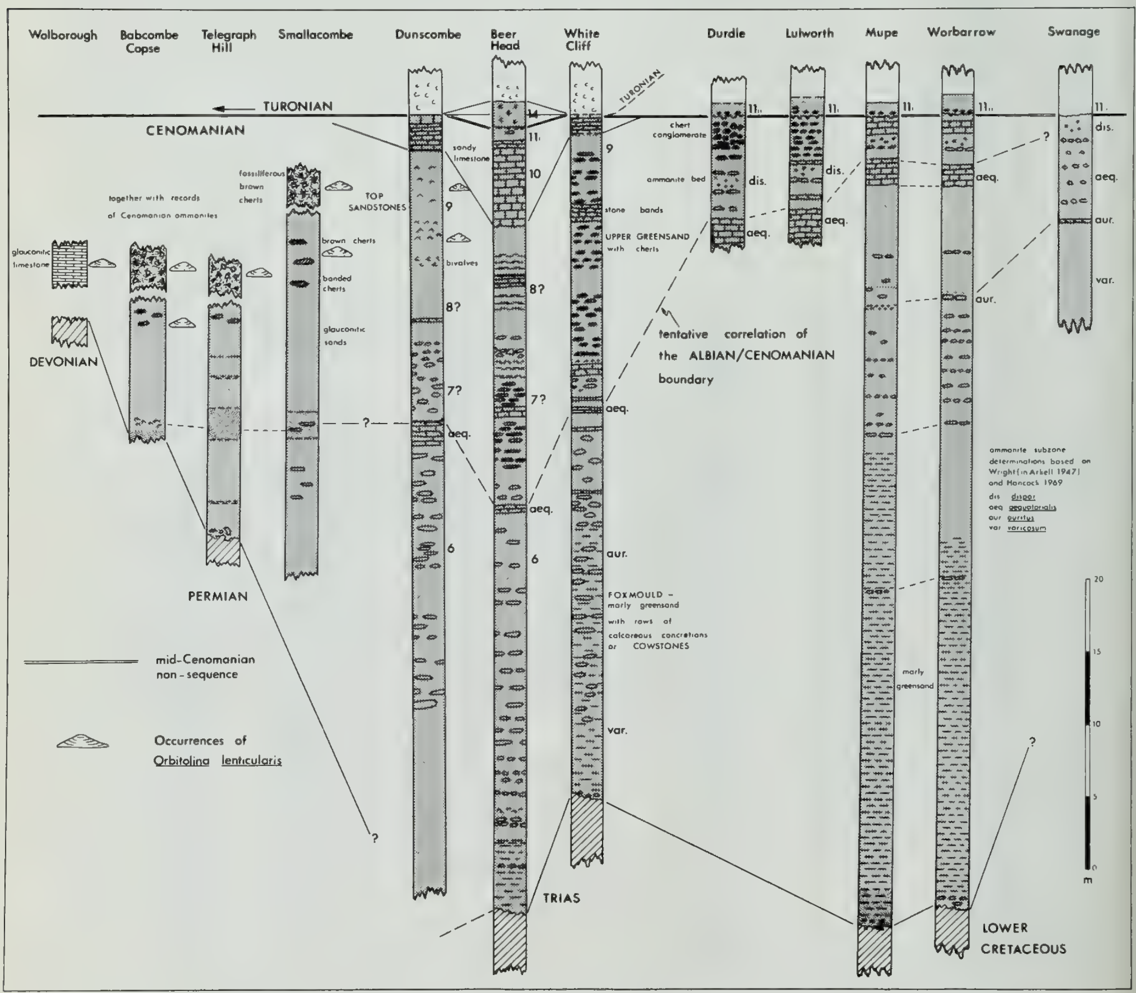

Wolborough
Babcombe Copse
Telegraph Hill
Smallacombe
Dunscombe
Beer Head
White Cliff
Durdle
Lulworth
Mupe
Worbarrow
Swanage
TURONIAN
CENOMANIAN
TURONIAN
together with records of Cenomanian ammonites
fossiliferous brown cherts
TOP SANDSTONES
brown cherts
banded cherts
glauconitic sands
glauconitic limestone
sandy limestone
bivalves
chert conglomerate
ammonite bed
stone bands
UPPER GREENSAND with cherts
tentative correlation of the ALBIAN/CENOMANIAN boundary
FOXMOULD – marly greensand with rows of calcareous concretions or COWSTONES
marly greensand
DEVONIAN
PERMIAN
TRIAS
LOWER CRETACEOUS
mid-Cenomanian non-sequence
Occurrences of Orbitolina lenticularis
ammonite subzone determinations based on Wright (in Arkell 1947) and Hancock 1969
dis dispar
aeq aequatorialis
aur auritus
var varicosum
11.
10
9
8?
7?
6
14
dis.
aeq.
aur.
var.
?
20
15
10
5
0
m

Fig. 46 A correlation of the Upper Greensand and associated strata along the south coast of England from Swanage (Dorset) to Newton Abbot (Devon).

conditions and age very like those pertaining in Cambridgeshire (Hart 1973a). While Wright uses the Dorset fauna to place the Cambridge fauna stratigraphically, we regard the 'ammonite bed' fauna, like the 'Cambridge' fauna, as totally derived. However, the *Exogyra* Sandstone underlying the 'ammonite bed' can be placed in the *auritus/aequatorialis* Subzone, indicating a greater hiatus than that developed in Cambridgeshire.

The Upper Greensand successions of Dorset and Devon are given in Fig. 46, which also includes the sections just discussed. The conclusions based on examination of the latter also apply to the whole cross-section. However, in south-east Devon there is also a substantial thickness of 'Top Sandstones', which have already been correlated with the Eggardon Grit, and shown to belong in the Lower Cenomanian. The chert conglomerate seen at Lulworth and Durdle Door is absent from Devon, and it is suggested that this concentrate, formed prior to the deposition of the Chalk Basement Bed, represents the Zone 10–Zone 11(i) interval (i.e. the Cenomanian Limestones of Devon). The upper levels of the Chert Beds and the whole of the Top Sandstones on the Devon coast yield specimens of *Orbitolina lenticularis* (our own collections; see also Jukes-Browne (1900 : 208) and the specimens P.43429 in the British Museum (Natural History)). These occurrences of *Orbitolina* can be traced through Wilmington and into the Rye Hill Sands of the Warminster area. In the latter a Cenomanian dating is agreed by all workers. The microfauna from the 'ammonite bed' of the Purbeck coast, as well as that from the Chert Beds at Standers Mill Plantation, indicate that the orbitolines from the Chert Beds are of Lower Cenomanian (Zones 7–8) age, and that the overlying Top Sandstones occupy the Zone 9 interval. The fauna of the Foxmould supports this determination: we have found Upper Albian faunal elements in it, although the actual zonal indicators are absent. The main objection to this dating relies on the much-quoted specimen of *M.* (*Mortoniceras*) of *stoliczkaia* type found in the Chert Beds near Charmouth (Kennedy 1970 : 642; Wilson *et al.* 1958 : 148; Spath 1933 : 423). Even if the provenance and identification of this specimen are accepted it is suggested that one ammonite from a single horizon is inadequate evidence for dating a whole formation covering the greater part of south-west England. This specimen's value is lessened by the presence of an abundant, derived *S. dispar* Zone fauna at approximately the same level to the east of Charmouth.

When the Cretaceous succession is traced westwards from Beer it becomes appreciably thinner until its only representative west of the River Exe is the series of sands and cherts forming the Haldon Hills. These beds, in part, appear to be the lateral equivalent of the Chert Beds of Dorset and SE Devon, although this relationship has yet to be confirmed palaeontologically. Hart (1971) suggested that the *Orbitolina lenticularis* fauna could be used for this purpose. As other evidence must also be considered and some of the sections in the Haldon Hills are not very well known, additional description is necessary.

The locality at Wolborough (Newton Abbot) was rediscovered by Dr R. A. Edwards during the I.G.S./Exeter University (1966–69) revision of the Teignmouth (Sheet 339) 1″ Geological Map. Although small and badly exposed it provides the only definite record of limestones from the Upper Greensand of the Haldon and Bovey areas (Fig. 47). These limestones are coarse-grained, sandy and glauconitic, and occur as blocks associated with shelly, glauconitic sands 400 m south of the church (SX 855699) at Wolborough. The section is only seen along a field boundary and its position in the succession is not certain, but recent excavations by Hamblin & Wood (pers. comm., and in press) in the Greensand sequence have revealed further details of the succession, and some firm correlations will soon be available. However, since the samples were collected only 4·5–5·0 m from an exposure of Devonian slates, it may be inferred that these limestones are very low in the local succession. To the north of Newton Abbot no limestones are seen in any part of the succession and the beds with *O. lenticularis* come from much higher levels in the sequence (see Fig. 46). The localities to the north of the Bovey Basin were first described by Godwin-Austen (1842). Later workers (Woodward 1876, Pengelly 1865) were unable to locate these sands and gravels precisely. Reid (1898) found them, but as they were close to the Bovey Basin they were ascribed to the Eocene. Jukes-Browne & Hill (1903) demonstrated the presence of Cenomanian fossils in the cherts found in the gravels at Aller Vale, and used them to postulate the presence of the Cenomanian sea in the Haldon area. The most useful locality at present is the large working sandpit operated by Kingston Minerals Ltd at Babcombe Copse (SX 869766)

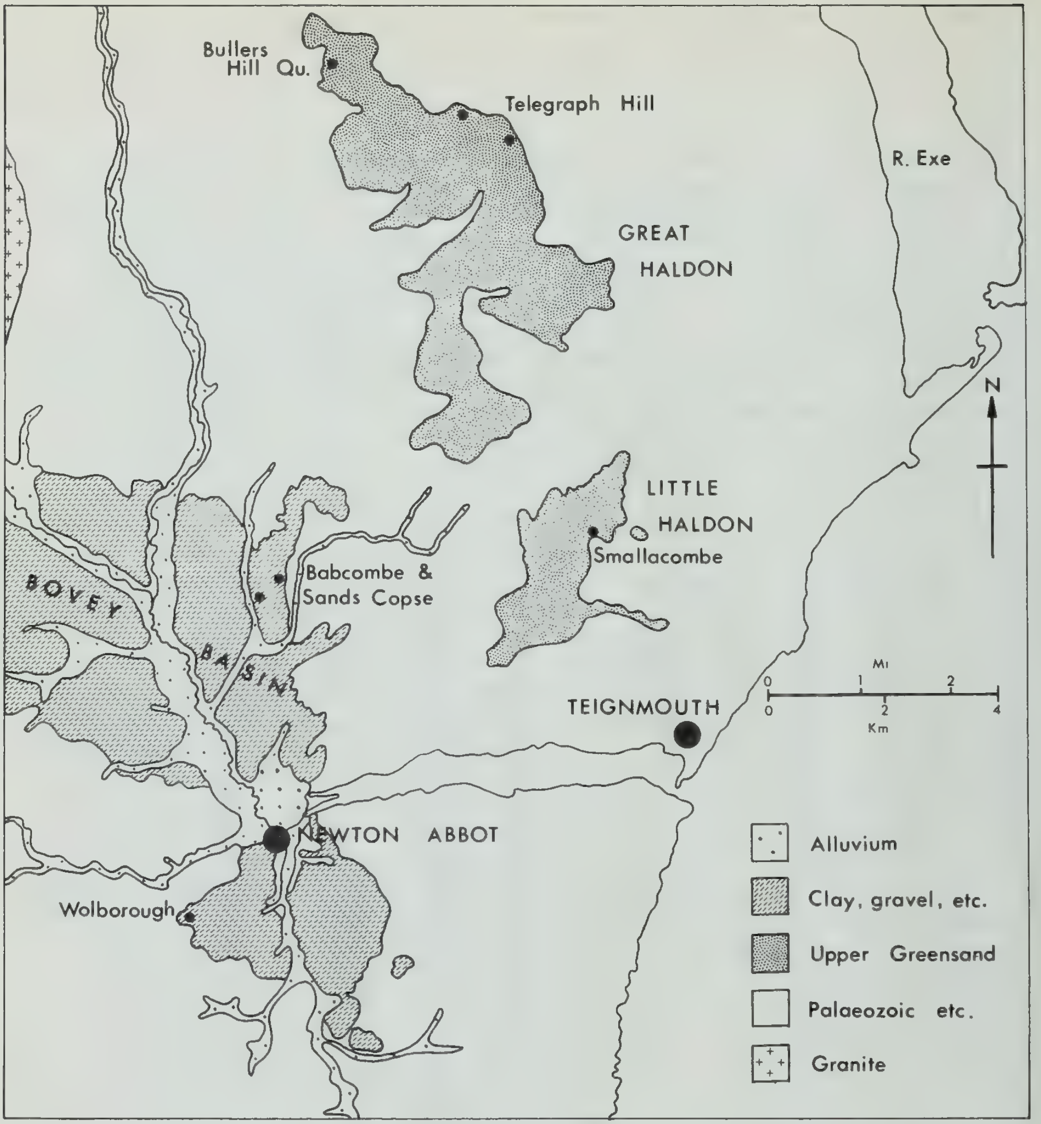

Bullers Hill Qu.
Telegraph Hill
R. Exe
GREAT HALDON
N
LITTLE HALDON
Smallacombe
Babcombe & Sands Copse
BOVEY BASIN
Mi
0 1 2
0 2 4
Km
TEIGNMOUTH
NEWTON ABBOT
Wolborough
Alluvium
Clay, gravel, etc.
Upper Greensand
Palaeozoic etc.
Granite

Fig. 47 Cretaceous localities in the Haldon Hills and Bovey Basin, south Devon. The Haldon Gravels (of Eocene and Pliocene age) have been omitted from this figure.

which is 400 m from Babcombe Farm (SX 867769). The lower levels of this pit display a series of gravelly sands which are overlain by slightly finer sands that contain pale grey banded cherts. Littering the floor and the tips of the quarry are brown-grey fossiliferous cherts that cannot be seen *in situ*. These appear to come from the overlying material and therefore cannot be placed in the succession with any accuracy.

The pits at Sands Copse (SX 865759), while providing occasional brown, fossiliferous cherts, are so degraded that no material can be collected *in situ*. At Bullers Hill Quarry (SX 882848) a succession of gravels can be seen resting on decalcified Upper Greensand, which appears to be impregnated with clay wash from above. Pale grey banded cherts can be found *in situ*, while the brown, fossiliferous cherts again litter the floor of the workings. The small pits on Telegraph Hill described by Jukes-Browne & Hill (1900) have been completely obliterated by the rebuilding of the Exeter–Torbay (A.380) road, although the temporary excavations for the main cutting allowed an inspection of the full succession down to the New Red Sandstone. A second phase of excavations for the Exeter–Plymouth (A.38) road have allowed the confirmation of the Telegraph Hill succession.

While exposures on Little Haldon are very poor, there are some accounts of them in the literature. The section up Smallacombe Goyle (SX 923767) was given in some detail by Jukes-Browne & Hill (1900 : 223). The *Orbitolina* fauna was recorded from the upper levels of the brown cherts, and this occurrence is confirmed here. These cherts appear very similar to those found in Babcombe Copse and therefore give an indication where the latter occur in the regional succession. Jukes-Browne & Hill (1900 : 226) also recorded *O. concava* (Lamarck) from the Basement Sands but this has not been confirmed. The coral fauna was thought by Jukes-Browne to occur in the upper levels of the lowest glauconitic sands in Smallacombe Goyle, and this provides an accurate link with the Blackdown Sands of the Honiton area. This relationship was discussed by Downes (1882) and little work has been done since then. The Blackdown Sands have yielded ammonites which place them in the *varicosum* and/or *orbignyi* Subzones (Hancock 1969 : 66). Unfortunately no microfauna can be obtained from this area, as these sands have been totally leached by percolating water owing to the early removal of the overlying chalk.

The relationship of these sequences to those on the Devon coast is shown in Fig. 46, which also indicates the recorded horizons of *O. lenticularis*. It must be emphasized that the majority of specimens of *O. lenticularis* have been obtained from blocks of cherts found on the floors of the various quarries in the area. The only *in situ* records are from Wolborough, where the limestones appear to be at their normal stratigraphic level, and Smallacombe Goyle. This latter occurrence, as already noted, shows the brown fossiliferous cherts in their true stratigraphic position. Thin-section studies of the cherts of both types from this area have proved the *Orbitolina* fauna to be in association with an abundant microfauna, now replaced by chert. *Hedbergella delrioensis* of Cenomanian aspect has been identified, although no zonal forms have been isolated so far. Three ammonites have been found in the brown fossiliferous cherts by Wood (1971 : 100). These have been identified as *Mantelliceras* sp., ? *Hyphoplites* cf. *pseudofalcatus* (Semenow) and *Turrilites* cf. *acutus* Passey – and are an admixture of Lower and Middle Cenomanian forms. While the *Mantelliceras* and *Hyphoplites* agree with our suggested dating of the Chert Beds in south-west England, the occurrence of *T. acutus* is a problem. Kennedy's (1969) *T. acutus* assemblage occurs above the mid-Cenomanian non-sequence, and we cannot explain this occurrence in the cherts. West of a line running south-east through Membury the only horizon in which elements of the *T. acutus* assemblage occur is in the basal layer of Cenomanian Limestone Bed C. This species has never been found in the lower two beds (A and B).

Two other lines of non-micropalaeontological evidence can be used to place the Haldon succession accurately in its stratigraphic position. The three levels at which instability affected the Lower and Middle Cenomanian are as follows:

i. Basal Cenomanian non-sequence (i.e. the Albian/Cenomanian boundary), which produced the 'ammonite bed' above the *Exogyra* Sandstone.

ii. The Zone 9/Zone 10 non-sequence, now thought to precede the Cenomanian Limestone succession, equating with the flexuring described by Smith (1957a, etc.).

iii. The mid-Cenomanian non-sequence which produced the Chalk Basement Bed and the base of Bed C of the Cenomanian Limestone succession.

While Hart (1971) suggested that the folding demonstrated on Haldon by Durrance & Hamblin (1969) equated with the mid-Cenomanian non-sequence, present research has shown that the trends are not compatible with this suggestion. It is more probable that the warping associated with the Zone 9/Zone 10 boundary equates with this level, thus agreeing with the suggestion of Durrance & Hamblin that the folding was early Cenomanian, prior to the deposition of the Cenomanian Limestones. The placing of the upper part of the Haldon succession in the Lower Cenomanian Zones 7–9 would agree with the occurrence of *Orbitolina* as well as two of the ammonites found by Wood.

The second line of evidence reinforcing this correlation results from work (Hart 1973b) with

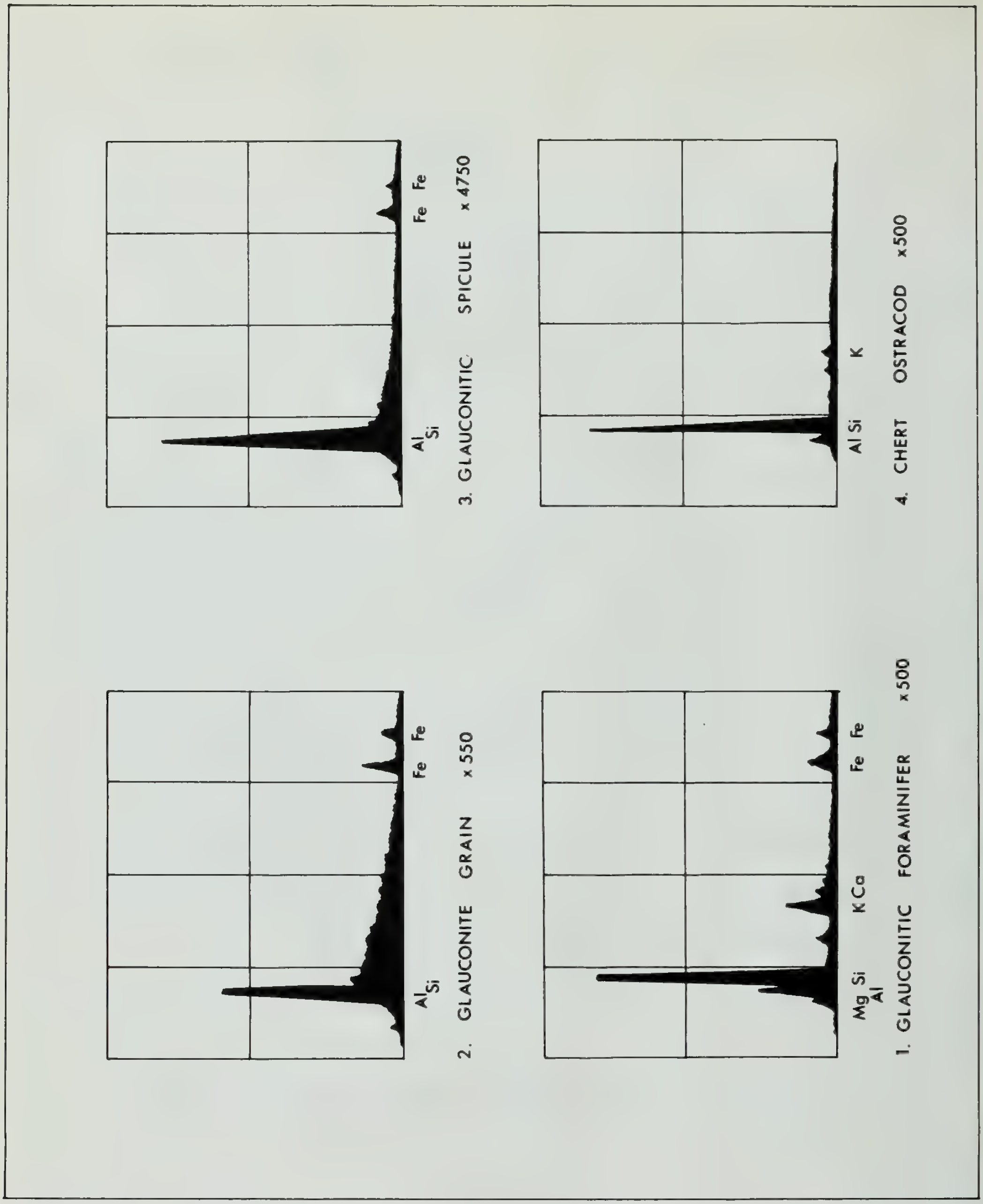


Fig. 48 Geochemical data of specimens from the Upper Greensand.
1. Glauconitic cast of a foraminifer.
2. Grain of glauconite from the sediment.
3. Sponge spicule replaced by glauconite.
4. Ostracod specimen from the cherts.

the Cambridge Instruments Stereoscan Mk II and Nuclear Diodes' EDAX 707 Dispersive X-ray analyser. The following summarizes some of the data from this study. Preliminary work included the analysis of some of the 'glauconitic' casts of foraminifera so commonly encountered in the sands and limestones of south-west England. Until recently substantial quantities of material were required for X-ray analysis, and since only good specimens were retained in our micropalaeontological collections, chemical determinations were not possible. However, the present instrumentation allows the analysis with little, if any, damage to the specimen involved. The profile obtained from one cast of *Rotalipora* from the Cenomanian sands – confirming the belief that the mineral is from the glauconite suite – is shown in Fig. 48(1). To provide a standard profile some glauconite grains from the sediment have also been analysed, and one of these is shown in Fig. 48(2). The glauconite cast is completely different in composition from that recorded in the grain. The most interesting aspect of the comparison is the richness of the cast in silicon. As the infilling of the chambers was presumably a post-depositional feature it is suggested that this is evidence of the presence of Si-rich post-depositional groundwater.

It has been noted that in the same sequence of strata sponge spicules are very abundant at some levels, particularly where beds of chert are lacking. Almost all these spicules have been replaced by glauconite, although the colour is slightly different from that seen in the foraminiferal casts. Analysis of individual spicules (Fig. 48(3)) has shown aluminium-rich glauconite very similar to that forming the mineral grains, and quite unlike anything found in the casts. This possibly indicates that the replacement of Si-rich sponge spicules with Al-rich, Si-poor, glauconite could not belong to the same generation as that found in the casts. The final stage of the investigation was to study the composition of the foraminifera and ostracods brushed from some of the cherts on Haldon. The profile shown in Fig. 48(4) is typical of any of these individuals, and it is interesting to note the occurrence of detectable amounts of potassium, reminiscent of the foraminifera profile in Fig. 48(1).

This analytical work suggests that there have been some substantial changes in the geochemistry of the sediment during diagenesis. The timing of these changes is quite important, and it has been possible to show that the level below which silicification took place was coincident with the mid-Cenomanian non-sequence. While glauconite casts, sponge spicules and evidence of silicification (cherts in the Upper Greensand and beekitization in the Cenomanian sands of Wilmington) are features of the succession up to the level of the mid-Cenomanian non-sequence, they are not seen above it. The effects above the Eggardon Grit (or Top Sandstones) are very slight, the main changes being in the succession below that level (i.e. Zones 7 and 8). This zonal determination coincides with the occurrence of abundant sponges in the Lower Cenomanian in south-east England, which characterizes the Zone 7–8 interval (see Fig. 12 and Fig. 17).

Clearly the question of the age of the Chert Beds cannot finally be decided at present, but it is hoped that the suggestions given above will stimulate further research into their stratigraphic position. Our overall interpretation of mid-Cretaceous stratigraphy in south-west England is not unlike that of many earlier workers (Hancock 1969; Kennedy 1970) and a compilation of both the microfaunal and macrofaunal data should allow a yet more accurate correlation. One fact that stands out in our work is the recognition of the importance of derived faunas. As Hart (1973a) has shown *à propos* the Cambridge Greensand, the presence of a completely diagnostic, but phosphatized *Stoliczkaia dispar* Zone fauna is no guarantee that there is any *S. dispar* Zone in the area. All over the south-west of England it is evident that macrofaunal data provide a succession up to and including the *auritus* and *aequatorialis* Subzones. Above that level the *S. dispar* Zone fossils come entirely from phosphatic concentrations (particularly on the Dorset coast), and are unreliable indicators of the age of the matrix. The *S. dispar* Zone is not at present thought to occur *in situ* in the SW Province, although new work by Hamblin & Wood (pers. comm.) may necessitate a reappraisal of this view.

c. North-east Province

North of the North Norfolk Swell from Hunstanton the mid-Cretaceous sequence is represented by thin, nodular chalk, some of which is pink, yellow, purple and green. Disaggregation of these

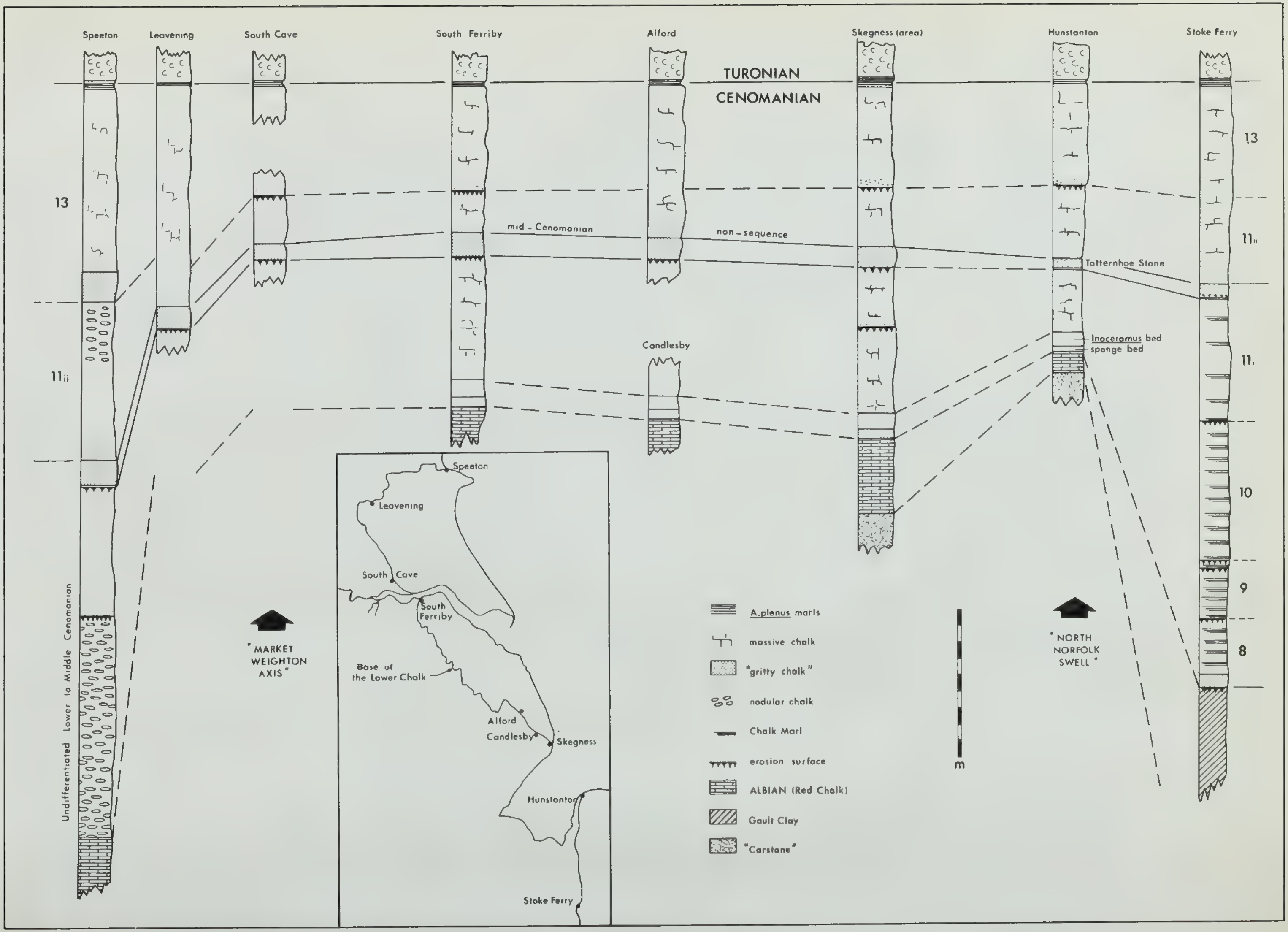

Speeton
Leavening
South Cave
South Ferriby
Alford
Skegness (area)
Hunstanton
Stoke Ferry
TURONIAN
CENOMANIAN
13
11ii
Undifferentiated Lower to Middle Cenomanian
mid - Cenomanian
non - sequence
Totternhoe Stone
Candlesby
Inoceramus bed
sponge bed
13
11ii
11i
10
9
8
"MARKET WEIGHTON AXIS"
"NORTH NORFOLK SWELL"
Speeton
Leavening
South Cave
South Ferriby
Base of the Lower Chalk
Alford
Candlesby
Skegness
Hunstanton
Stoke Ferry
A.plenus marls
massive chalk
"gritty chalk"
nodular chalk
Chalk Marl
erosion surface
ALBIAN (Red Chalk)
Gault Clay
"Carstone"
m

Fig. 49 The correlation of the mid-Cretaceous from Speeton (Yorkshire) to Stoke Ferry (Norfolk).

materials is difficult and detailed micropalaeontological investigation has not been attempted. Some indications of the stratigraphy can be gleaned from the general lithological sequences and the microfaunal data already obtained. The Plenus Marl horizon is used, as in southern England, although the 'Black Band' has not yet yielded any microfauna. The mid-Cenomanian non-sequence can be shown to coincide with the upper surface of the Totternhoe Stone, and is therefore a recognizable horizon. The Totternhoe Stone appears as a thin, shelly, glauconitic limestone, while some distance above it another gritty bed of limestone equates with the level of Jukes-Browne's Bed 7 (see Fig. 17, p. 70). The available microfaunal data confirm this suggestion.

Although the overall correlation of the NE Province (Fig. 49) is very similar to that shown by Jeans (1968), microfaunal data permit a tighter correlation with the south-east of England. The area between Hunstanton and Leavening is shelf, north (Speeton) and south (Cambridgeshire) of which thicker sequences are recorded. More recently Jeans (1973) has reinvestigated the Market Weighton axis, and shown that basement faults apparently controlled the Cretaceous sedimentation.

d. North-west Province

Although the distribution proves a much wider initial coverage, the mid-Cretaceous of Northern Ireland and western Scotland occurs as small isolated patches of arenaceous deposits. M. B. H. obtained very little microfaunal data from these deposits.

In western Scotland (Bienn Iadain and Lochaline (Morvern); Carsaig, Loch Don, Alt na Teangaidh and Gribum (Mull); Clach Alasdair (Eigg) and Strathaird (Skye)) the macrofaunal evidence (Lee & Bailey 1925, Richey 1961) and the meagre microfaunal evidence give a Lower Cenomanian age for the glauconitic sandstones. The succession on Bienn Iadain (glauconitic sandstones, white sandstones, brown clays) is completely referable to the Cenomanian. In Scotland, as in Northern Ireland, there is a hiatus in the Turonian. In Northern Ireland the evidence shows in addition a period of intra-Cenomanian erosion preceding the main break in deposition. Here the lowermost unit of the mid-Cretaceous succession, the Glauconite Sands, contains a diagnostic Lower Cenomanian fauna (Hancock 1961, McGugan 1957, and our own collections), and equates with the glauconitic, calcareous sandstones of the Morvern succession. The Glauconite Sands of Northern Ireland grade upwards (Portmuck, Colin Glen, etc.) into the Yellow Sandstones that have been dated as Cenomanian (? Middle) by Hancock (1961). The intra-Cenomanian contact between the Yellow Sandstones and the overlying Upper Glauconite Beds is interesting in that it is picked out by a level of erosion and piping. The fauna of the Basement Sands (Zone of *Exogyra columba*) of the Upper Glauconite Beds is Cenomanian (Hancock 1961) and it is suggested tentatively that this intra-Cenomanian erosion surface relates to the mid-Cenomanian non-sequence. The occurrences of *Orbitolina concava* (Lamarck), recorded by Hancock (1961 : 18) and Hume (1897) from the Basement Sands, have not been verified, and no examples of this species have been found in the Museum collections.

If the mid-Cenomanian non-sequence can be placed in the Northern Ireland succession, it may be possible to relate it to the succession in Scotland. The evidence already suggests the non-sequence to be responsible for the termination of sedimentation prior to the Turonian hiatus. If this is borne out by future work, it would be possible to correlate the mid-Cretaceous arenaceous sediments of the NW Province directly with those in the Lower Cenomanian (Zones 7–9, ? 10, ? 11(i)) of the south-east of England.

e. Mid-Cretaceous of northern France

The sections at Cap Gris Nez are so similar to those at Dover that they have been studied in less detail than those farther along the French coast, at Cap d'Antifer (Seine Maritime). The latter extend from St Jouin to just east of the Cap, where a small valley allows access to the beach. This section (Fig. 50) has been described by Juignet (1970), whose ammonite determinations are accepted here. This cliff section is very different from those in the Lower Chalk of south-east England. The chalk contains very little clay material – unlike the Chalk Marl – while flints and cherts occur in large numbers. Hardgrounds, with associated phosphatized faunas, occur at

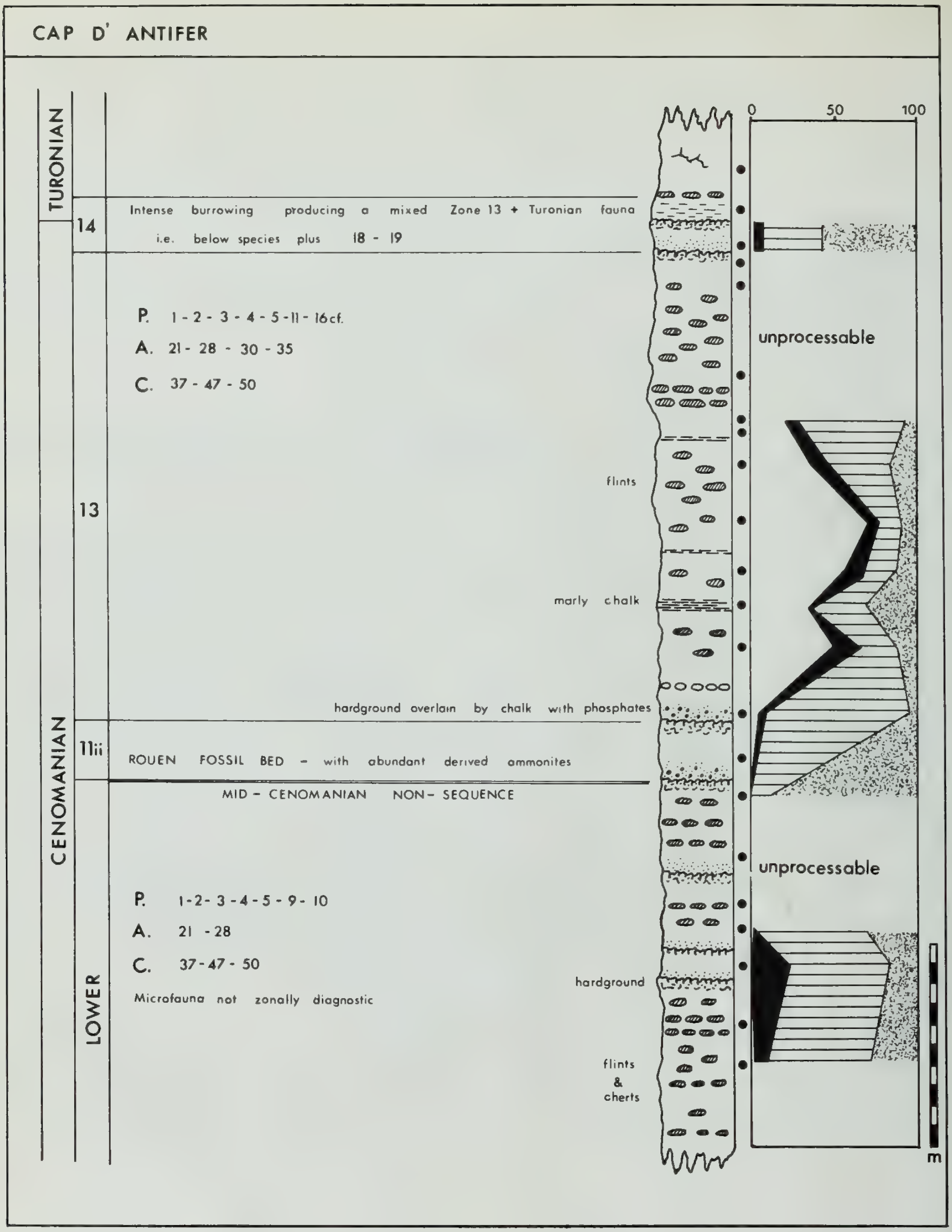

CAP D' ANTIFER
TURONIAN
CENOMANIAN
LOWER
14
13
11ii
Intense burrowing producing a mixed Zone 13 + Turonian fauna
i.e. below species plus 18 - 19
P. 1 - 2 - 3 - 4 - 5 - 11 - 16cf.
A. 21 - 28 - 30 - 35
C. 37 - 47 - 50
flints
marly chalk
hardground overlain by chalk with phosphates
ROUEN FOSSIL BED - with abundant derived ammonites
MID - CENOMANIAN NON - SEQUENCE
P. 1 - 2 - 3 - 4 - 5 - 9 - 10
A. 21 - 28
C. 37 - 47 - 50
Microfauna not zonally diagnostic
hardground
flints & cherts
0
50
100
unprocessable
unprocessable
m

Fig. 50 Microfaunal details, Cap d'Antifer, Seine Maritime, France. The ornamentation used in the planktonic/benthonic ratio graph is explained in Fig. 12c. See Fig. 20 for key to letter code.

regular intervals and are reminiscent of the erosion surfaces in the Cenomanian Limestones. Although the microfauna has not been studied in detail it fits into the British microfaunal zonation. The thickness of the Cenomanian at Cap d'Antifer is approximately 40 m, which is a marked reduction from the 76–78 m recorded at Dover. The most prominent feature of the succession east of Cap d'Antifer is the phosphate bed which is the lateral equivalent of the mid-Cenomanian non-sequence. It was equated with the Rouen fossil bed by Juignet. It contains a Zone 11(ii) microfauna, and we agree with Juignet's correlation. Immediately above this horizon at Cap d'Antifer there is another hardground which is followed by 13 m of chalk with flints. The fauna of this chalk is of Zone 13, which agrees with Juignet's (1970) suggestion that it belongs to the Middle and Upper Cenomanian. The upper hardground also marks the appearance of pyrite nodules in the Cenomanian succession, thus agreeing with their appearance in Britain close to the base of Zone 13. The *Actinocamax plenus* Subzone is represented by two thin limestones higher up the succession. Below and between them are phosphatized hardgrounds. The lower hardground corresponds to the sub-*plenus* erosion surface of Jefferies (1962, 1963), while the upper horizon appears to represent the pre-Bed 4 erosion surface of the British succession. The occurrence of *Metoicoceras gourdoni* (de Grossouvre) in the upper limestone bed agrees with this microfaunal determination. The central hardground is therefore the Cenomanian/Turonian boundary on the basis of the zonation proposed here.

The Lower Cenomanian below the mid-Cenomanian non-sequence at Bruneval Plage and St Jouin contains flints and cherts, both of which occur in bands that can be traced laterally for some distance. The cherts occur below the mid-Cenomanian non-sequence, and not above. Since the Chert Beds in south-west England have been assigned a post-diagenetic origin, initiated at the time of the mid-Cenomanian non-sequence, this fact may be significant. The lower levels of the succession have not been sampled in detail and no firm zonal determinations have been suggested.

We have accepted the correlation of Rouen with Cap d'Antifer proposed by Juignet (1970). At Côte Ste Catherine the famous Rouen 'Fossil Bed' represents the mid-Cenomanian non-sequence, with its associated Basement Bed fauna of derived ammonites. The Cenomanian chalk above this hardground is only some 2·0 m thick, and is overlain by a layer of glauconitized pebbles which represent derived remnants of the *A. plenus* Subzone (Jefferies 1963; Kennedy & Hancock 1970). The microfauna (Fig. 51) of this chalk is completely in accord with a Zone 13 determination. This apparently conflicts with the published data, which indicates a Middle Cenomanian age for the Rouen Chalk. Kennedy & Hancock (1970) state that the Fossil Bed at Rouen is younger in aspect than at Snowdon Hill (Chard) (Fig. 34, p. 91), but they compared accumulations of derived ammonites representing a larger part of the Middle–Upper Cenomanian interval. The chalk above the Basement Bed at Chard is of Zone 13 age, as at Rouen. The Cenomanian fauna disappears completely at the base of the line of glauconitized pebbles, which represents the Cenomanian/Turonian boundary. We would disagree with Jefferies' (1963) suggestion that the main erosion level was that below the line of pebbles. A much greater hiatus is represented by the Fossil Bed – at the level of the mid-Cenomanian non-sequence.

A traverse south-west of Rouen nearer to the type area of the Cenomanian (Fig. 1) has been described by Juignet (1971 : fig. 4) and this can be placed in our microfaunal succession with little difficulty. The most interesting aspect of Juignet's work is the detection of an 'axis of sedimentation' running south-east through Le Merlerault. The Lower Cenomanian succession of the 'Craie Glauconieuse' appears similar on both sides of this axis, while the overlying Middle and Upper Cenomanian sequence is completely different. To the north of the 'axe de Merlerault' the Middle and ? Upper Cenomanian is in the 'Craie de Rouen' facies which continues to the Channel coast. To the south-west of it the succession is considerably thicker, and the change is comparable to that seen when crossing the North Norfolk Swell from north to south. The Upper Cenomanian is represented by the 'Sables du Perche' and the 'Marnes à Huîtres'. The mid-Cenomanian non-sequence in the Sarthe is immediately overlain by the 'Craie de Théligny', which is especially well developed in the area to the north-east of Le Mans. At Les Aulnais, near Théligny, the phosphatized fossil bed, typical of the non-sequence, rests on a very resistant calcareous sandstone which is reminiscent of the Eggardon Grit of the south-west of England. The faunal relationships are almost identical with those at Eggardon Hill in Dorset (Fig. 40). To the south of Le

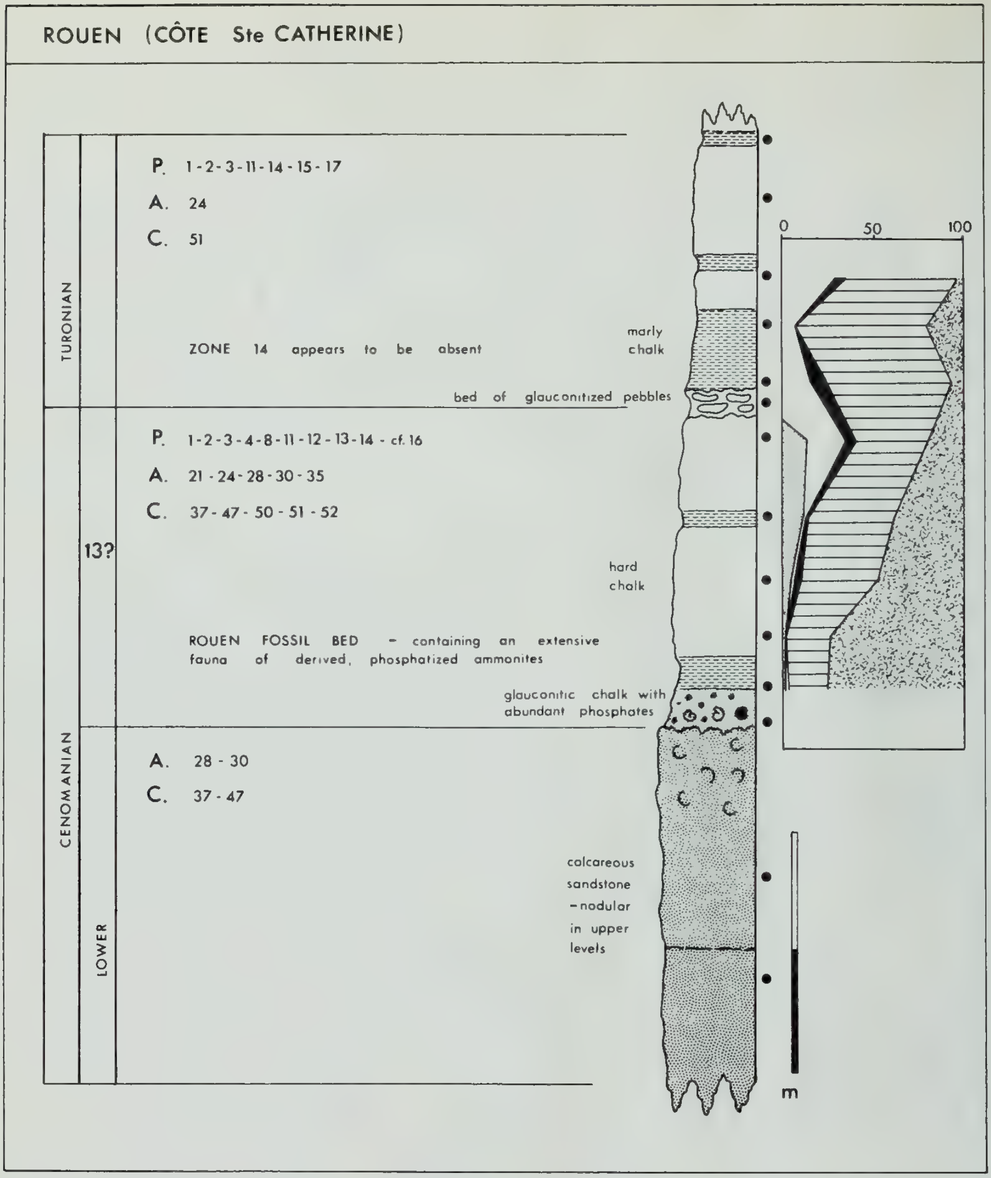

ROUEN (CÔTE Ste CATHERINE)
TURONIAN
P. 1-2-3-11-14-15-17
A. 24
C. 51
ZONE 14 appears to be absent
marly chalk
bed of glauconitized pebbles
CENOMANIAN
13?
P. 1-2-3-4-8-11-12-13-14 - cf. 16
A. 21 - 24 - 28 - 30 - 35
C. 37 - 47 - 50 - 51 - 52
hard chalk
ROUEN FOSSIL BED – containing an extensive fauna of derived, phosphatized ammonites
glauconitic chalk with abundant phosphates
LOWER
A. 28 - 30
C. 37 - 47
calcareous sandstone – nodular in upper levels
0
50
100
m

Fig. 51 Microfaunal details, Côte Ste Catherine, Rouen, France. The ornament used in the planktonic/benthonic ratio graphs is explained in Fig. 12c. See Fig. 20 for key to letter code.

Mans the mid-Cenomanian non-sequence is lost in the complex successions of the 'Sables de Maine'. The Upper Cenomanian of this area has already been discussed in the section on the Cenomanian/Turonian boundary.

The most interesting feature of the 'axe de Merlerault' is that its trend is almost parallel to those plotted in the south-west of England, and appears to belong to the same structural suite. The same trends appear again in north-east France where both Jefferies (1963) and Robaszynski (1971) have described the succession in the quarry behind the station at Bettrechies, 4 km north-west of Bavay (Nord). The 'Sarrazin de Bellignes' was regarded as Middle Cenomanian by Marlière (1939 : 356, fig. 36; 1965) while Robaszynski places it within the Lower Cenomanian. The overlying 'Tourtia de Mons' contains a microfauna which indicates a position within Zone 14(i–iia). The overlying chalk contains elements of a Turonian fauna, and was included within the 'couches à grosses globigérines' by Robaszynski (1971). The relationships are very similar to those at Membury where a 'tourtia' is overlain by glauconitic chalk containing a Zone 14(i–iia) fauna. At Membury the underlying greensand may be comparable with the Sarrazin, although we have no faunal data from this level. The two successions are compared in Fig. 52. It is significant that *Inoceramus labiatus* first appears 1 m up the succession at Bettrechies. The position of the first appearance of *I. labiatus* at Membury is not known as there is a gap in the exposures at this critical level.

Marlière (1965) suggested that the 'Tourtia de Mons', when traced into the centre of the Anglo-Paris Basin, could be equated with the Totternhoe Stone. This correlation has proved correct, but we place the mid-Cenomanian non-sequence at the upper surface of the Totternhoe Stone and not the base, as indicated by Marlière.

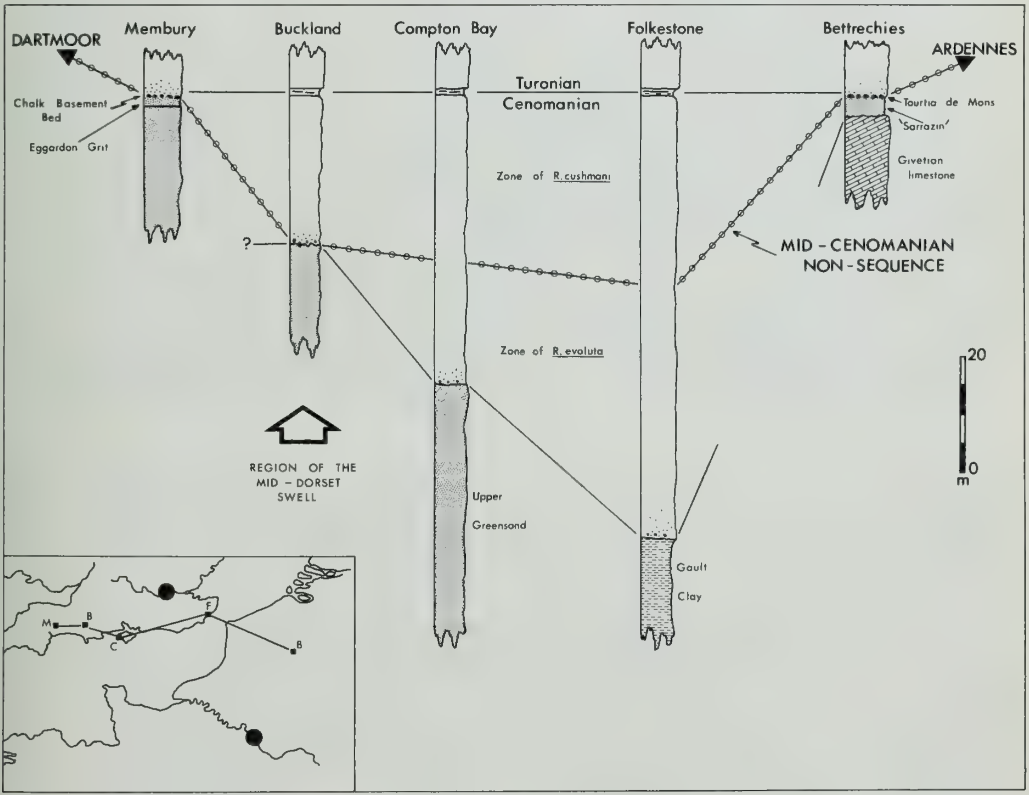

DARTMOOR
Membury
Buckland
Compton Bay
Folkestone
Bettrechies
ARDENNES
Turonian
Cenomanian
Chalk Basement Bed
Eggardon Grit
Tourtia de Mons
'Sarrazin'
Givetian limestone
Zone of R. cushmani
?
MID - CENOMANIAN NON - SEQUENCE
Zone of R. evoluta
20
0
m
REGION OF THE MID - DORSET SWELL
Upper Greensand
Gault Clay
M
B
C
F
B

Fig. 52 Submergence of the Dartmoor and Ardennes Massifs.

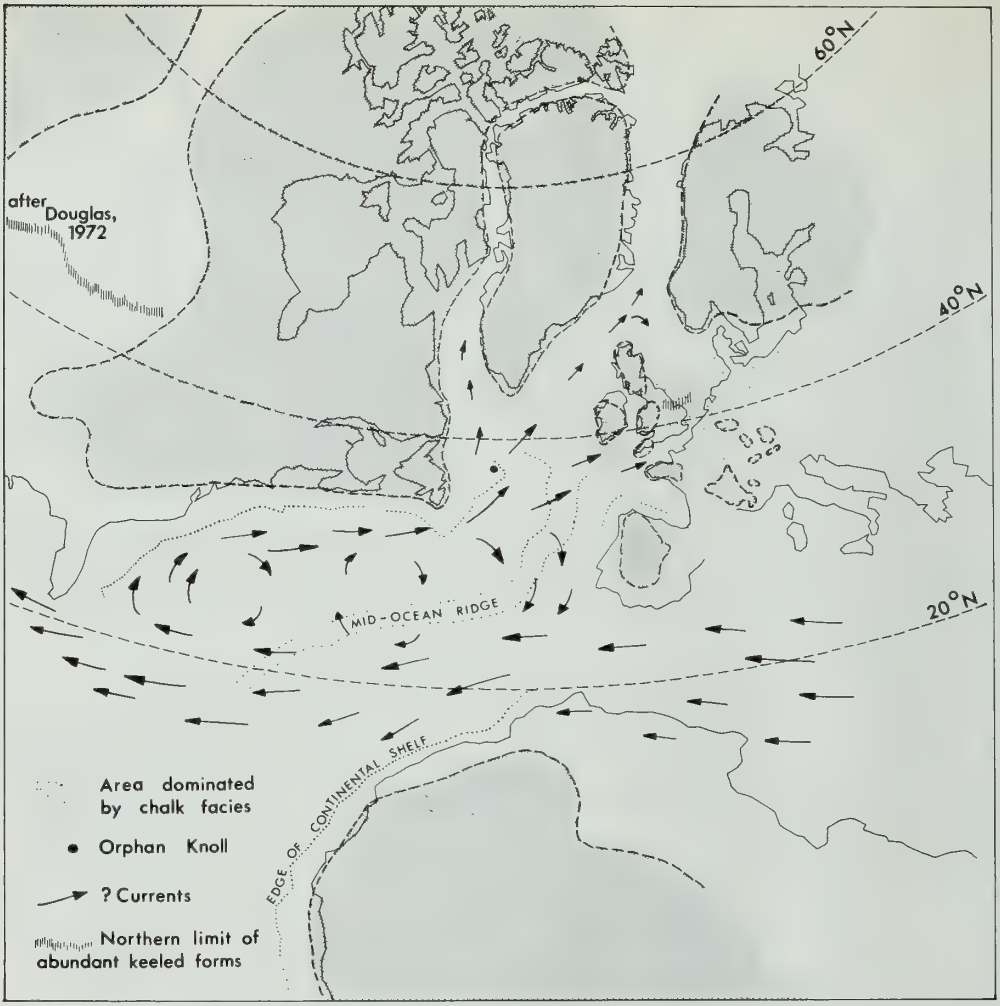

after Douglas, 1972
60°N
40°N
20°N
MID-OCEAN RIDGE
EDGE OF CONTINENTAL SHELF
Area dominated by chalk facies
Orphan Knoll
? Currents
Northern limit of abundant keeled forms

Fig. 53 Upper Cenomanian palaeogeography of the North Atlantic Ocean and surrounding areas (base map from Hart & Tarling 1974). The palaeocurrents are based on the work of Luyendyk *et al.* (1972), modified by the present authors in the light of palaeontological information (Hart & Carter 1975).

The mid-Cenomanian non-sequence has been traced successfully across the whole of the Anglo-Paris Basin from central France to northern England, and from East Anglia to Devon. The following section attempts to relate the work in NW Europe to more speculative studies of the development of the North Atlantic Ocean.

Mid-Cenomanian changes in North Atlantic palaeogeography

The important changes occurring at the level of the mid-Cenomanian non-sequence in NW Europe probably relate to the development of the North Atlantic Ocean. Dr D. H. Tarling (University of Newcastle) has kindly provided the authors with a reconstruction of the Cenomanian (100 Ma) North Atlantic Ocean based on palaeomagnetic data. This is shown in Fig. 53. The discussion pertinent to the reconstruction is included in a separate account (Hart & Tarling 1974). This reconstruction has been used to plot the approximate positions of the Cenomanian shorelines (based on the mid-Cenomanian). Britain and France are seen to fall in the centre of a large island-studded shelf area which lay at about 40°N. In a synthesis of the palaeogeography the following items are relevant.

i. The planktonic/benthonic ratio

This subject has already been discussed (11-62-65) and no further comments will be added.

ii. The occurrence of the keeled planktonic foraminifera

In modern oceans keeled planktonic foraminifera are generally restricted to regions within the 17 °C surface water isotherm. Bandy (1967) plotted '*Globotruncana/Rotalipora*' lines through the Upper Cretaceous, north (or south) of which keeled planktonic individuals have not been recorded in large numbers. Bandy related this distribution to the palaeotemperature work of Urey *et al.* (1951), Lowenstam & Epstein (1954) and Bowen (1961), all of which was based on data from NW Europe. This shows that in the mid-Cenomanian the British area was at the temperature limit for keeled planktonic individuals. However, in modern oceans the 17 °C surface water isotherm usually lies within the latitudes 20°N and S, although it may extend to 40°N and S in areas affected by oceanic currents. Bandy (1967) indicated that in the European Cenomanian keeled forms extend into latitudes as far north as 48°N, although they are recorded in large numbers from East Anglia at latitude 52°N. While this suggests that there is some variance in the Cenomanian between the postulated temperature control or the latitude and the distribution of keeled forms, this is largely cancelled out in our palaeogeographical reconstruction, which places southern England in the region of 40°N. The rapid increase in the palaeotemperatures for the Turonian appears to have been initiated in the mid-Cenomanian, and while possibly attributable to the general warming reported in the Upper Cretaceous, it may be related in part to other factors.

The British planktonic occurrences originally lay very close to the 40° northern limit, and probably relate to the abundance variations of keeled and non-keeled forms recorded in the Cenomanian (Fig. 12). Two possible causes for these variations can be suggested. The first involves slight climatic oscillation, while the second, more likely, is the periodic influx of warm water into the European area. The effect of even slight movements would, in such borderline conditions, be sufficient to cause a local influx of keeled individuals. In the Middle Cenomanian only isolated peaks of keeled forms are recorded; they become more persistent in the Upper Cenomanian. In the Turonian a steady population of keeled forms is recorded, even though Britain and Europe were drifting northward at the time.

The evidence suggests that (i) the depth increase recorded in the mid-Cenomanian allowed the influx of warmer oceanic water by drowning the marginal zone of islands shown in the palaeogeographical reconstruction, and (ii) that the water masses flowed into this area intermittently at first, but later became more constant.

iii. Phytoplankton production

Tappan's work on phytoplankton productivity (1968) shows a slight increase in the production of calcareous phytoplankton in the mid-Cenomanian. In modern oceans areas of rapid phytoplankton increase occur where mixing of water masses takes place. This is particularly true in the North Atlantic, off Newfoundland, where the Gulf Stream impinges against the cooler water emerging from the Labrador Sea. The area of greatest coccolith concentration in surface sediments forms a spur towards the European area, with high figures shown off the Portuguese coast. The production of organic carbon also shows a high in the north-east Atlantic Ocean. Both of the latter occur where the warmer water impinges on the shelf water of NW Europe, and it is possible that similar factors were operating in the Upper Cretaceous.

The Upper Cretaceous deposits of NW Europe (particularly of Great Britain and France) consist of considerable thicknesses of coccolith ooze, now in the form of chalk. This concentration could be attributed to the influx of warm water into an embayment of a shelf sea in temperate latitudes.

iv. Calcimetry of the Cenomanian

Destombes & Shepard-Thorn (1971) have provided data on the calcimetry of the Lower Chalk of the south-east of England as part of the Channel Tunnel Site Investigation. Their work has shown that $CaCO_3$ percentages of 80–95% are attained only above the mid-Cenomanian non-sequence, although there is an increase from 50–70% below that level. Once the level of 90% is attained, above the non-sequence, it is held, with minor fluctuations, at that level throughout the remainder of the Upper Cretaceous. The relationship of the calcimetry increase to the postulated increase in phytoplankton production is quite striking.

v. Faunal diversity

Valentine & Moores (1970) have shown it possible to relate faunal diversity to plate movements. On the break-up of Pangaea in the Triassic the standing level of diversity in the fragments increased steadily throughout the Jurassic, but less rapidly in the Late Jurassic and Early Cretaceous. In the mid-Cretaceous (c. 100 Ma) which, according to Valentine & Moores (1970), coincided with a widespread transgression, another sharp increase in the standing level of diversity occurred. This latter increase is traceable as starting at about what is now the level of the mid-Cenomanian non-sequence. Such a change could be expected to coincide with a depth increase and the development of a different ocean circulation pattern, particularly when the newly-forming South Atlantic Ocean is considered.

vi. Coiling directions in planktonic foraminifera

The coiling direction of planktonic species, particularly *Globorotalia pachyderma* (Ehrenberg) and *Globorotalia truncatulinoides* (d'Orbigny), have been used for the correlation of Pleistocene oceanic sediments. In general terms the greater the percentage of dextrally coiled individuals the warmer the water conditions prevailing, and *vice versa*. In the Cenomanian, there is an admixture of coiling directions, although the majority of individuals in the Upper Cenomanian are dextral. Both the *Rotalipora cushmani* and *R. greenhornensis* populations follow this rule, while the *Praeglobotruncana* spp. population is more variable. In the Lower Cenomanian the latter (largely *P. delrioensis*) is 50% dextral, while the Upper Cenomanian population (largely *P. stephani*) is generally 90% dextral. The groups that evolved from this stock (*P. algeriana*, *P. hagni* and *Globotruncana* spp.) are also similarly coiled. Although the change from 50% to 90% dextral coiling in *Praeglobotruncana* spp. appears gradual, it is initiated above the level of the mid-Cenomanian non-sequence. This is also true of *R. cushmani*, as populations from immediately above the non-sequence show a lower percentage of dextrally coiled individuals than ones from nearer the Cenomanian/Turonian boundary.

The planktonic/benthonic ratios, distribution of the keeled planktonics, calcimetry, faunal diversity and the changes in coiling direction of planktonic species all indicate that although an island barrier to NW Europe existed in the Lower Cenomanian, it was greatly reduced at the time of, and just after, the mid-Cenomanian non-sequence. The reduction of this barrier would have provided access for warmer, oceanic water, and the gentle subsidence of the whole shelf area would have allowed the continuation of marine sedimentation characterizing the Upper Cretaceous of NW Europe. This is the reverse of the situation in Colorado described by Eicher (1969a), where the evidence suggests that the seaway began to silt up in the Turonian. Fig. 11 (p. 62), shows the correlation between Eicher's Colorado succession and the Isle of Wight (Culver Cliff) sequence. The Zones of *Rotalipora cushmani* and *R. evoluta* in the two sections can be directly correlated, as can the change to a predominantly planktonic population in the mid-Cenomanian. In Britain the calcareous, plankton-rich succession continues into the Turonian while the sequence in Colorado indicates a gradual disappearance of plankton-sustaining conditions, and a reversion to clastic sedimentation.

The data also suggests a warming of the Cenomanian sea in NW Europe above the mid-Cenomanian non-sequence. Supporting evidence is now available from the Deep Sea Drilling Project cores in the North Atlantic area. Site 111 (Leg 12) at Orphan Knoll (NE of Newfoundland) provides an interesting section through the mid-Cretaceous (Laughton *et al.* 1970, Laughton *et al.* 1972, Ruffman & van Hinte 1973, van Hinte, Adams & Perry 1975). In the core, the Albian and Lower Cenomanian sandy limestones (with *Rotalipora evoluta*) are overlain by Maastrichtian chalks. The hiatus occurs at possibly our Zone 9/Zone 10 non-sequence, or more probably the more important mid-Cenomanian non-sequence. Several workers (e.g. Ewing *et al.* 1970a, Hayes *et al.* 1971, Vogt *et al.* 1971, Habib 1970) have discussed the mid-Cretaceous sedimentation of the proto-Atlantic Ocean, and Vogt *et al.* have postulated an oceanic current system in the eastern Atlantic during the Lower Cretaceous (Fig. 53). It is considered that the depth increase postulated for the mid-Cenomanian, and the resulting Cenomanian 'transgression', not only ultimately drowned the islands shown in Fig. 53, but also allowed the development of water circulation across the drowned crest of the mid-Atlantic ridge. The passage of warm water over the Newfoundland Banks area could have produced a strong current through the relatively narrow straits between Spain and North America. This would then have produced the phosphatized hardground and the stratigraphic hiatus recorded at Orphan Knoll. With the opening of the Labrador Sea later in the Upper Cretaceous, water movement could have been deflected away from Orphan Knoll by a southward flow between Greenland and Canada. Mixing of the warm Atlantic water with the cooler southward-moving stream might have provided the stimulus to phytoplankton growth required to produce the Maastrichtian chalks recorded at Orphan Knoll.

It is impossible to say at present if part of the moving water mass turned southwards forming a true gyre. There seems to have been little influx of cold water into the main body of the Atlantic Ocean, as the first arrival of cold Norwegian water marked by the appearance of the cherts in the sea-floor sediments does not occur until the Lower–Middle Eocene (Ewing *et al.* 1970b). The currents in the Upper Cretaceous would also be affected by the flow of water through the Central American isthmus which was to remain open well into the Tertiary.

In NW Europe, during Late Cretaceous times, warm waters must have flowed from the southwest into an embayment (lat. 30°–45°N) into which there must have been some supply of cooler, nutrient-rich water (from the north ?). This, on upwelling adjacent to the nearby coastline, would have stimulated phytoplankton production, and so induced carbonate sedimentation.

Although there is insufficient evidence to prove that the North Atlantic current pattern was initiated in the mid-Cretaceous, there is an indication of fundamental changes at that time which affected the whole Upper Cretaceous history of NW Europe. Work on this problem is still in progress, but it is hoped that this interim report may be of some value in our understanding of the stratigraphy of the Cretaceous System in this area.

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A. W. H. Bartram

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Summary

The fishes placed in the holostean family Macrosemiidae by a succession of authors have been re-examined. The group has been found to be polyphyletic. With the removal of four of the genera (*Uarbryichthys*, *Ophiopsis*, *Songanella* and *Aphanepygus*) and one species (*Macrosemius maeseni*), the remainder form a monophyletic group based upon two unique specializations. The genus *Enchelyolepis* is too poorly known to be assigned to the macrosemiids with certainty but it is provisionally retained in that family here. *Uarbryichthys* is shown to have acquired one unique specialization in parallel with *Macrosemius*, and is placed in a new family Uarbryichthyidae, the sister-group of the Macrosemiidae. These two groups are halecostome neopterygians in the sense of Patterson (1973), but show no evidence of relationship with either of the two main halecostome groups, the Halecomorphi or the Teleostei. Neither can the Macrosemiidae be shown to belong to any other halecostome group, and thus the family is classified as Halecostomi, subdivision *incertae sedis*.

Legnonotus krambergeri sp. nov. is described.

Introduction

The holostean fish family Macrosemiidae was established long ago by Thiollière (1858). Woodward (1895) gave a formal description of the group and considered them related to the Caturidae, and no subsequent worker has seriously questioned this view. Saint-Seine (1949) published the most detailed account to date of some members of the family. However, the bones of the skull of these fishes are so delicate that adequate preparative techniques are needed for their structure to be properly interpreted. For this reason, acetic acid preparation has been used in this investigation.

The primary aim of the present study has been to establish the Macrosemiidae as a monophyletic group, if possible, on the basis of shared, unique specializations. The remaining specializations of the family have been compared with those of other actinopterygians, to place the macrosemiids within a cladistic scheme of relationships and to see whether Woodward was right in deriving them from the caturids.

Unfortunately, this study has been hampered by two factors. Firstly, specimens of macrosemiids are comparatively rare. Secondly, the number of specimens available for acetic acid preparation was limited. Consequently, it has been impossible to give a full account either of the anatomy of most of the species, or of the variation between individuals within a species. Nevertheless, it is hoped that enough new information has been obtained for the objectives outlined above to have been reached.

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Geological occurrence

The Macrosemiidae are extinct. The latest known members of the family, *Notagogus pentlandi* and *Propterus scacchi*, occur in the Lower Cretaceous (Barremian–Albian) of Pietraroia, Benevento and Castellamare, Italy. *Notagogus parvus* is present in the Lower Cretaceous (Wealden) of Bernissart, Belgium, while *N. ferreri* and *Propterus vidali* are found in the Neocomian of Lerida, Spain. The earliest known macrosemiids belong to the genus *Legnonotus*, from the Upper Triassic; *L. krambergeri* occurs at Hallein (Austria) and *L. cothamensis* is present in the Rhaetic of Gloucestershire. All the other macrosemiid species have been recovered from Upper Jurassic deposits of Europe. A brief discussion of the ecological conditions obtaining at the time of their deposition is given in the Ecological Note, pp. 225–6.

Uarbryichthys, which has been removed from the macrosemiids and classified as the plesiomorph sister-group of this family, occurs in the freshwater Jurassic deposits of New South Wales.

Techniques

Most macrosemiids have been collected from the Lower Kimmeridgian Lithographic Limestones of Eichstätt and Cerin. These matrices disintegrate in dilute acetic acid, and in the present work about a dozen specimens from the former locality have been prepared by the transfer technique of Toombs & Rixon (1959). These specimens were then examined with the aid of reflected and transmitted light, and of radiography.

Once the structure of the fishes had become familiar by the use of this technique, mechanical preparation could be used to advantage in the examination of specimens from other localities.

Systematic descriptions

Infraclass **NEOPTERYGII** (*sensu* Patterson 1973)

Division **HALECOSTOMI** (*sensu* Patterson 1973)

Subdivision ***incertae sedis***

Family **MACROSEMIIDAE** Thiollière 1858

Diagnosis. Small to large, laterally-compressed halecostome fishes; infra- and supraorbital sensory canals anastomosing behind the eye; supratemporals excluded from the midline; supratemporal commissure borne on the parietals; frontals forming an open trough housing the supraorbital canal over the ethmoidal region; nasals trough-like; rostral reduced to a short tube; vomer paired and toothed; parasphenoid toothless, forming basipterygoid processes and a pedicel at the entrance to the posterior myodome; exoccipital surrounding vagus foramen; epioccipital lining lateral cranial canal; sclerotic unossified; antorbital forming a tube around the infraorbital canal; nine infraorbitals, of which the first seven are scroll-like and the last two tubular; dermosphenotic fixed to skull roof; supraorbitals none to several; suborbitals absent; hyomandibular inclined anteroventrally, with head in the form of a quadrant facing anterodorsally and outer face of shaft forming an elongated flange alongside the anterior edge of the preopercular; symplectic short, and remote from mandible; metapterygoid in form of a disc lacking a large anterodorsal segment; two palatines and ectopterygoid toothed; gape small, the jaw articulation lying below or anterior to the orbitosphenoid; premaxillae immobile, with slender nasal processes; supramaxillae absent; mandible short, and deep at the level of the coronoid process, ventral border deeply concave, sensory canal housed in trough formed by dentary and angular; articular and retroarticular ossifying from Meckel's cartilage; quadratojugal long, stout, sometimes fusing distally with the quadrate; preopercular bent sharply forward beneath the orbit, the sensory canal exposed by large fenestrae; opercular tall and narrow with a convex lower border in contact with the subopercular; interopercular small and remote from lower jaw; seven or eight branchiostegals, the last three or four acinaciform; gular absent; hypohyal single; distal ceratohyal deep posteriorly; six supraneurals above anterior vertebrae, neural spines paired in caudal region, intermuscular bones absent; serrated appendage (clavicle?) present in pectoral girdle; dorsal fin long, divided in some genera; caudal fin forked or rounded, eight rays emanating from below the axial lobe, no epaxial fin-rays, uppermost fin-ray continuing into a scale row of the axial lobe, ural neural arches not elongated; scales rhomboid or cycloid, not broader than deep in ventral region; main lateral line terminating at base of axial lobe of caudal fin.

Genus ***MACROSEMIUS*** Agassiz 1844

Diagnosis. Large, elongate macrosemiid fishes; skull roof free from ganoine; supratemporals greatly reduced; cephalic division of main lateral line and supratemporal commissure exposed by large fenestrae; vomers bearing a transverse row of stout pointed teeth and a pair of large blunt teeth; ventral parts of anterior three infraorbitals expanded and overlapping the maxilla; gape very small, the quadrate articulation lying in front of the orbit; premaxilla with a single row of about four stout teeth; dentigerous expansion of maxilla shallow, upper and lower borders approximately parallel, the upper border forming a deep notch; maxillary teeth few and small; mandible with a single row of stout pointed teeth on dentary, prearticular and single coronoid bearing stout mammiliform teeth; palate fully ossified, ectopterygoid bearing about six tall stout teeth, two dermopalatines bearing similar teeth; anterodorsal edge of metapterygoid forming an obtuse angle; tooth plates on gill-arches bearing few, stout teeth; leading edge of preopercular forming sharp angle; opercular and subopercular ornamented with small, discrete tubercles of ganoine; uppermost branchiostegal ray devoid of ganoine; abdominal vertebral centra forming thick cylinders; pectoral fin with about 16 rays and six proximal radials, leading ray reduced to an unpaired spine, no fringing fulcra; pelvic fin formed by six rays preceded by a few small splints, fringing fulcra absent; anal fin profile convex, base extended, supported by six jointed, branching rays and an unjointed leading ray preceded by small splints, no fringing fulcra; caudal fin rounded, lower border armed with massive, median basal fulcra followed by fringing fulcra, small denticles on all rays except uppermost two or three, between three and five rays inserting onto the axial lobe, fringing fulcra on the uppermost fin-ray; dorsal fin single, extending from the occiput to the base of caudal fin, with between 32 and 39 rays each bearing denticles, leading ray preceded by two basal fulcra, fringing fulcra absent; region immediately on either side of dorsal fin devoid of scales; scales rhomboid, secondary transverse rows intervening between primary rows above the lateral line, scales below lateral line forming a pattern of rectangles.

Type species. *Macrosemius rostratus* Agassiz 1844.

INTRODUCTION. The genus *Macrosemius* was erected by Agassiz (1844) to contain a single species, *M. rostratus*, from the Lower Kimmeridgian of Bavaria. Thiollière (1873) recorded this species at the same horizon at Cerin (Ain, France), together with a new species, *M. helenae*. Sauvage (1883) described a very small form, *M. pectoralis*, from the Portlandian of Meuse, France. Woodward (1895) added two further species to the genus; these had previously been named *Disticholepis dumortieri* and *D. fourneti* by Thiollière (1873). Woodward also added *M. andrewsi* from the English Purbeck, and Eastman (1914a) described *M. dorsalis* from Bavaria. Woodward (1918) later transferred both *M. pectoralis* and *M. andrewsi* to a new genus, *Enchelyolepis*. Saint-Seine (1949) returned *M. dumortieri* and *M. fourneti* to Thiollière's genus *Disticholepis*. Later, Saint-Seine (*in* Saint-Seine & Casier 1962) described *M. maeseni* from the Upper Jurassic of Zaïre.

REMARKS. *Disticholepis* is very similar to *Macrosemius* and, following Woodward, is synonymized with that genus here. Eastman's *M. dorsalis*, founded upon a single specimen, probably belongs to *M. rostratus*, although, as he points out, the dorsal fin is taller than is usual for *rostratus*. *M. helenae* is synonymous with *Notagogus margaritae*, and *M. maeseni* is placed in the chondrostean genus *Tanaocrossus* Schaeffer (p. 207).

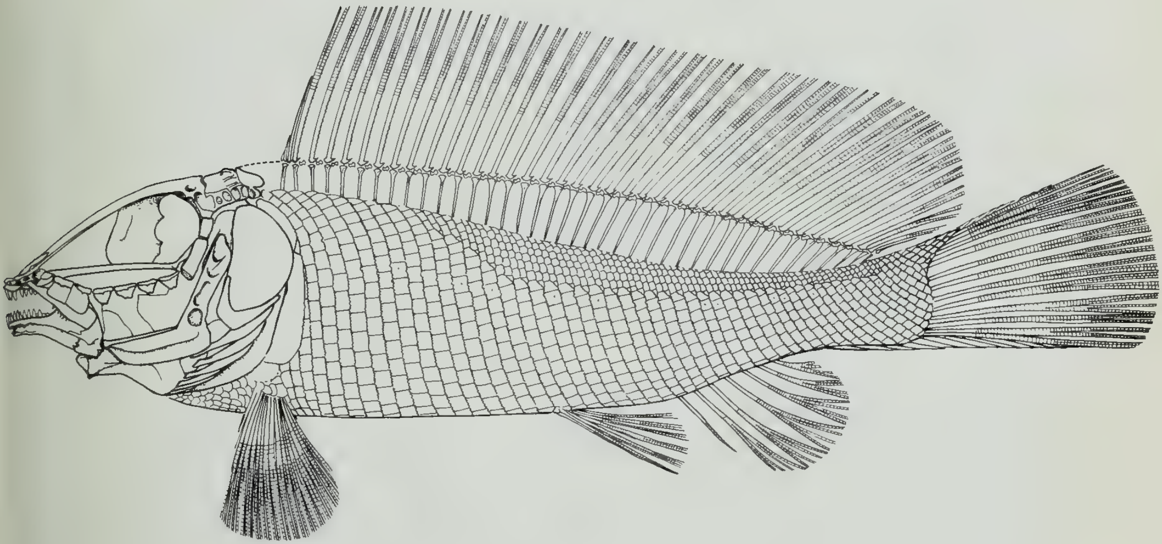

Fig. 1 *Macrosemius rostratus* Agassiz. Restoration of skeleton. ×½ approx.

Macrosemius rostratus Agassiz 1844

Figs 1–18; Pls 1–2

1836 *Macrosemius* Agassiz **2** : pl. D, fig. 3.
1844 *Macrosemius rostratus* Agassiz **2**, 2 : 150; pl. 47a, fig. 1.
1851 *Macrosemius latiusculus* Wagner : 74.
1851 *Macrosemius rostratus* Agassiz; Wagner : 73.
1863 *Macrosemius rostratus* Agassiz; Wagner : 647.
1863 *Macrosemius insignis* Wagner : 648; pl. 2.
1887 *Macrosemius latiusculus* Wagner; Zittel : 218, text-fig. 232.
1895 *Macrosemius latiusculus* Wagner; Woodward : 163, text-fig. 29.
1895 *Macrosemius rostratus* Agassiz; Woodward : 177; pl. 3, fig. 4.
1914a *Macrosemius rostratus* Agassiz; Eastman : 406; pl. 63, fig. 2.
1914a *Macrosemius dorsalis* Eastman : 406; pl. 65, fig. 2.
1966 *Macrosemius rostratus* Agassiz; Schultze : 275, text-figs 16b, 30.

DIAGNOSIS. *Macrosemius* with between 32 and 39 dorsal fin-rays; large basal fulcra along ventral border of caudal peduncle possessing straight edges; supraorbitals absent.

HOLOTYPE. Národnì Muzeum, Prague, T858, from the Eichstätt region of Bavaria.

HORIZON AND LOCALITIES. Lower Kimmeridgian of the Eichstätt and Kelheim regions of Bavaria.

MATERIAL. BM(NH): 37094, 37051, P7177, P956, P955, P3616; RSM: 1901.67.1; CM: 4453, 4765; Ei: 2 specimens; Mü: AS.1.769, AS.1.770, AS.1.640, AS.1.639, AS.6.24, 1954.1.530, 1904.1.18.

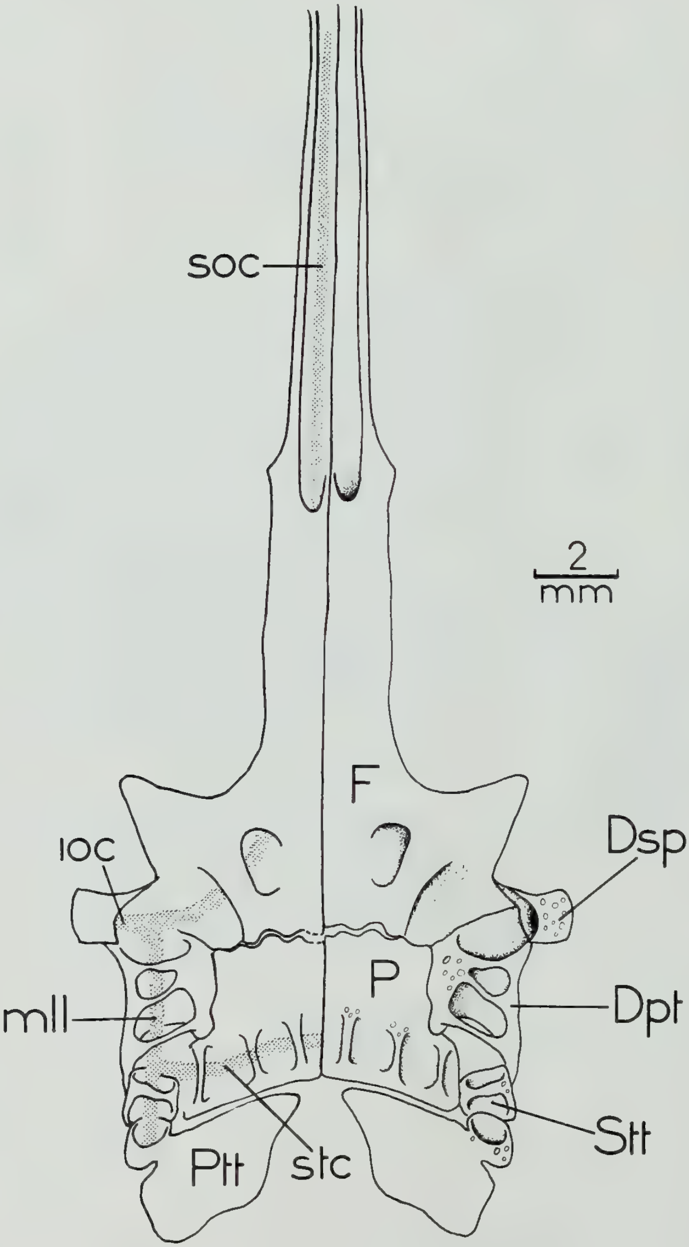

Fig. 2 *Macrosemius rostratus* Agassiz. Restoration of the skull roof of an immature individual, 37094.

DESCRIPTION. (i) General features. *M. rostratus* is a large, elongate fish reaching a standard length of about 220 mm. The trunk is shallow and tapers gradually to form a relatively deep caudal peduncle (Fig. 1).

(ii) Skull roof and braincase. As in the other members of the family, the postorbital region of the skull is short and compact. The form and relationship of the skull roof bones are displayed in 37094 (Fig. 2), although this individual is young (standard length 105 mm) and the bones may not have attained the adult pattern.

The frontals are constricted above the orbits and drawn out along the ethmoidal region. The parietals form a sinuous, non-overlapping suture with the frontals. The supratemporal commissure crossed the posterior part of the parietal; a delicate arch of bone, which spanned the canal, is preserved close to the midline, and the remains of another, lateral, arch may also be seen (Fig. 5). In older individuals these arches probably thickened only slightly, leaving the wide sensory canal exposed by large fenestrae; these are visible in specimens of *M. fourneti*, in which three such arches occur. The bases of the arches are perforated by small pores.

The supratemporal is a small, paired bone, excluded from the midline, forming a short tube around the cephalic section of the lateral line between the post-temporal and dermopterotic; the outer wall of the tube is reduced to a narrow strut. The supratemporal did not enclose the lateral part of the supratemporal commissure; the latter presumably joined the lateral line between the supratemporal and the dermopterotic. As is well known, the supratemporals of neopterygians arise in ontogeny as a transverse row of separate ossifications; in *Amia* and most extant teleosts, these fuse together to form paired supratemporals in the adult. In a few genera, however, the ossifications remain separate, as in *Lepisosteus*, *Sinamia* and *Dapedium*, for example. Jarvik (1967 : 191; fig. 5) has noted that in certain cypriniform teleosts the supratemporals fuse with the parietals, and that in rare individuals of *Polypterus* and *Acipenser* (1967 : fig. 6) fusion occurs between the medial supratemporal and the parietal. McDowell (1973 : 12) has since noted that in many other groups of teleosts (Notopteridae, Osteoglossoidei, Characidae, Gymnotidae) the supratemporal commissure is carried by paired bones which have hitherto been called parietals. The possibility exists, then, that a similar fusion has occurred in macrosemiids, and that the supratemporal commissure is borne by a compound parieto-supratemporal, rather than by a parietal which has come to occupy the hindmost part of the skull.

The dermopterotic extends along the lateral edge of the parietal and forms a suture with the frontal anteriorly. The cephalic portion of the lateral line occupied most of the width of the bone and was exposed by two large fenestrae bounded by three struts of bone. The sensory canal presumably joined the supraorbital canal in the space above the suture between the frontal and the dermopterotic, before turning downwards into the dermosphenotic as the infraorbital canal.

The lateral margin of the frontal forms a narrow tapering process over the posterior part of the orbit. The orbital embayment is very deep in this specimen; it was probably less marked in older individuals. Viewed from above, the frontal narrows further anteriorly, becoming very slender in the preorbital region. The supraorbital sensory canal passed into the frontal above the posterior limit of the orbit. The canal was exposed dorsally by a large fenestration as it passed through the bone toward the midline; the orbital wall of the canal is perforated by fine pores in this region (Fig. 5). The frontal forms a wide trough in the preorbital region, along which lay the supraorbital canal.

The right nasal is preserved in 37094 in a damaged condition (Fig. 8b). It formed a scroll around the anterior part of the supraorbital canal over the nasal process of the premaxilla. The rostral is not preserved in any of the specimens.

The vomer is paired and extends beneath the parasphenoid from the level of the orbitosphenoid, widening to form a broad contact with the dentigerous part of the premaxilla (Fig. 8b). The dorsal surface of the vomer in this region is shaped to receive the medial process of the maxilla. The vomerine teeth are visible in AS.1.770. A row of four stout, closely-set teeth occurs immediately posterior to, and parallel with, the premaxillary tooth-row. Each vomer bears in addition a large, laterally-compressed crushing tooth close to the midline behind the transverse row.

The left half of the braincase is incompletely preserved in medial view in specimen AS.1.640 (Fig. 3). The parasphenoid extends anteriorly from the basioccipital condyle and tapers to form

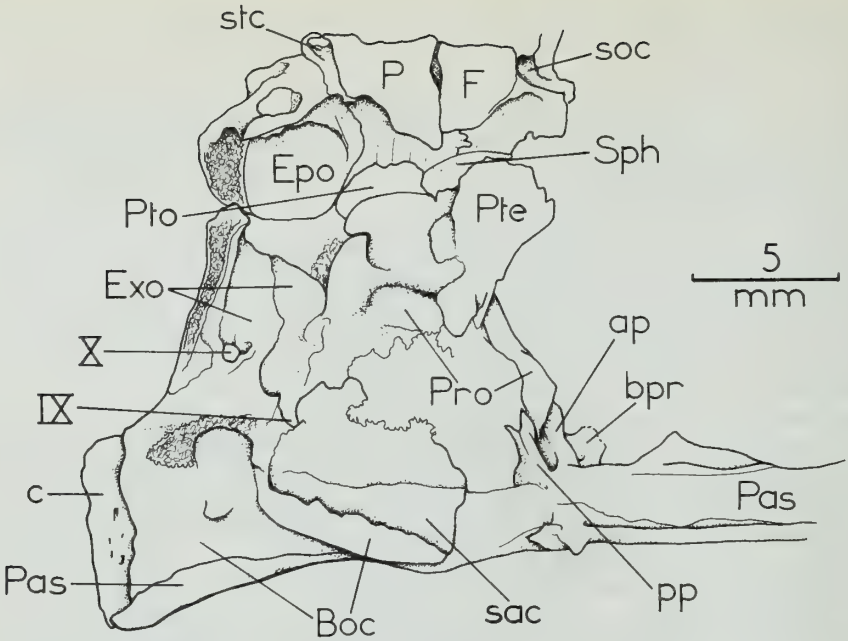

Fig. 3 *Macrosemius rostratus* Agassiz. Interior of the postorbital region of the braincase, as preserved in AS.1.769.

two prongs beneath the nasal processes of the premaxillae (Fig. 8a). The lateral edges of the parasphenoid below the orbit are marked by a deep longitudinal incision. Immediately posterior to this incision project a pair of stout basipterygoid processes, each with a shallow groove along the dorsal surface. The efferent pseudobranchial artery passed through a small canal ventral to the base of the process.

The basipterygoid process is united by a web of bone to the ascending process of the parasphenoid, which is inclined dorsolaterally and slightly posteriorly, supported by a thin buttress of bone (Fig. 5).

A short, stout pedicel, weakly forked at the tip, arises from the parasphenoid between the basipterygoid processes; this pedicel divides the entry of the posterior myodome into two. A small process has been reported in a similar position on the parasphenoids of the palaeoniscid *Kansasia eatoni* (Poplin 1974 : fig. 8) and of pholidophorid and leptolepid teleosts (Patterson 1975 : 517–27; figs 142–3).

The basioccipital is a massive bone beneath the foramen magnum whose floor, as usual, it forms. The first vertebral centrum appears to have been firmly fixed to the basioccipital condyle. Beneath the otic region the basioccipital forms the ventral part of a large, inflated, thin-walled chamber, supported along its ventral surface by a lateral expansion of the parasphenoid. This chamber housed the sacculus, which thus extended down to the level of the parasphenoid as it did, probably primitively, in *Australosomus* (Nielsen 1949 : fig. 9), *Pteronisculus* (Nielsen 1942 : fig. 14), *Lepisosteus* (Fig. 46) and *Amia*.

A posterior myodome almost certainly existed, the posterior rectus muscles passing into it on either side of the parasphenoid pedicel. Their origin was probably restricted to the deep recesses in the parasphenoid immediately posterior to the basipterygoid processes. Unfortunately the roof of the myodome, which would have formed from the prootics, is not preserved.

The glossopharyngeal nerve passed through a small foramen which pierces the posterior part of the wall of the saccular chamber in the basioccipital.

The exoccipital is partially fused at its base with the basioccipital and meets the posterior edge of the prootic; the vagus foramen is completely enclosed by the bone, as in *Lepisosteus* and

Lepidotes (Rayner 1948). A gap, cartilaginous in life, occurs between the dorsal edges of the exoccipital and prootic, and the epioccipital.

The epioccipital appears to be preserved in its natural position, with the exposed, medially-facing edge revealing cancellous endochondral bone. The internal wall of the epioccipital is approximately circular and forms a smooth surface; this indicates that, unlike the condition in *Amia*, the bone lined a cranial cavity. The epioccipital of *Lepisosteus* is similarly smooth (Rayner 1948: fig. 34) since it lines a large lateral cranial canal (Patterson 1975: fig. 111; Fig. 46). Rayner (1948 : 300) had sought for such a canal in larval *Lepisosteus* but reported its absence.

The lateral cranial canal of *Lepisosteus* occurs as usual in the wall of the braincase between the three semicircular canals. It is lined by cartilage except where this has been replaced by the epioccipital bone. It forms a connection with the median cranial cavity by means of a wide opening passing through the loop of the posterior semicircular canal, and of a much narrower tube passing through the loop of the anterior semicircular canal. The lateral cranial canal of *Lepisosteus* is filled with fatty tissue, as is the posterior part of the median cranial cavity; such tissue must increase the buoyancy of the fish. A lateral cranial canal has been recorded in *Caturus*, *Dapedium* (Rayner, 1948: figs 9, 15) and pholidophorids (Patterson 1975), but not in *Amia*. In teleosts, the medial wall of the lateral cranial canal fails to ossify in leptolepids (Patterson 1975: 413), and the canal is lost in living teleosts. But in living teleosts the inner face of the epioccipital is smooth (Allis, 1903: fig. 8; Goodrich 1930: fig. 599) and lines part of the cranial cavity. It is not known whether the smooth inner face of the epioccipital in *Macrosemius* lined a lateral cranial canal as in *Lepisosteus*, a primitive condition, or a part of the cranial cavity as in teleosts, a derived condition.

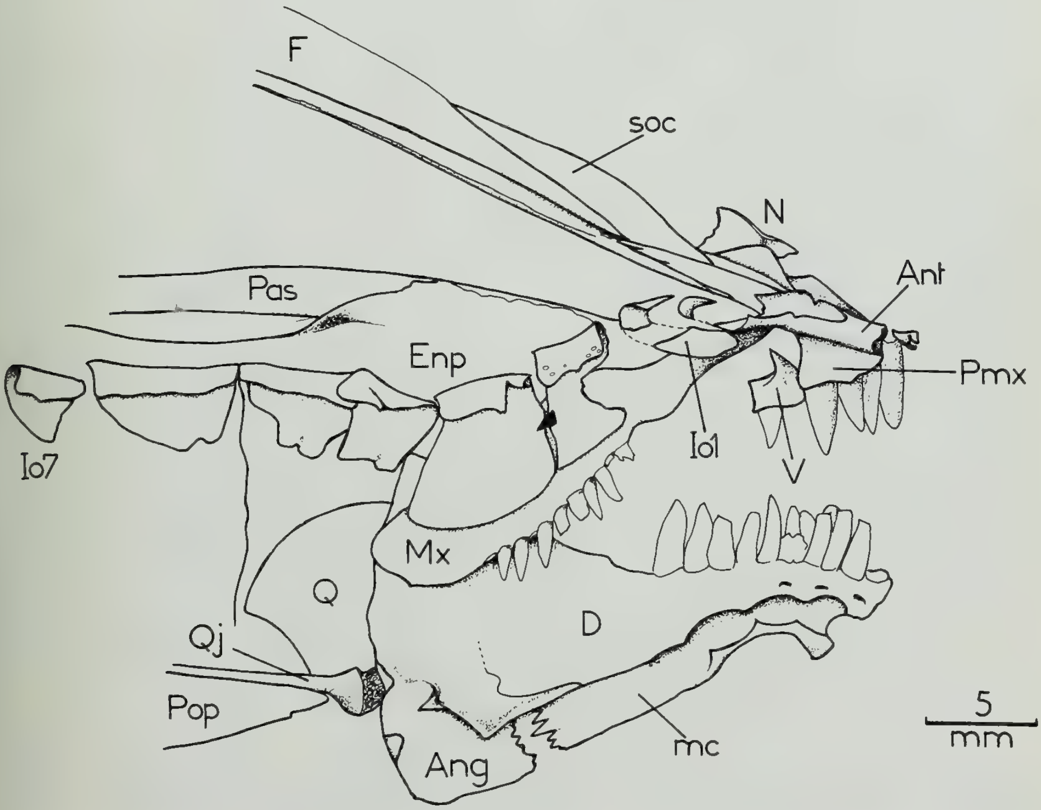

Fig. 4 *Macrosemius rostratus* Agassiz. Jaws and snout region in lateral view, as preserved in 37051.

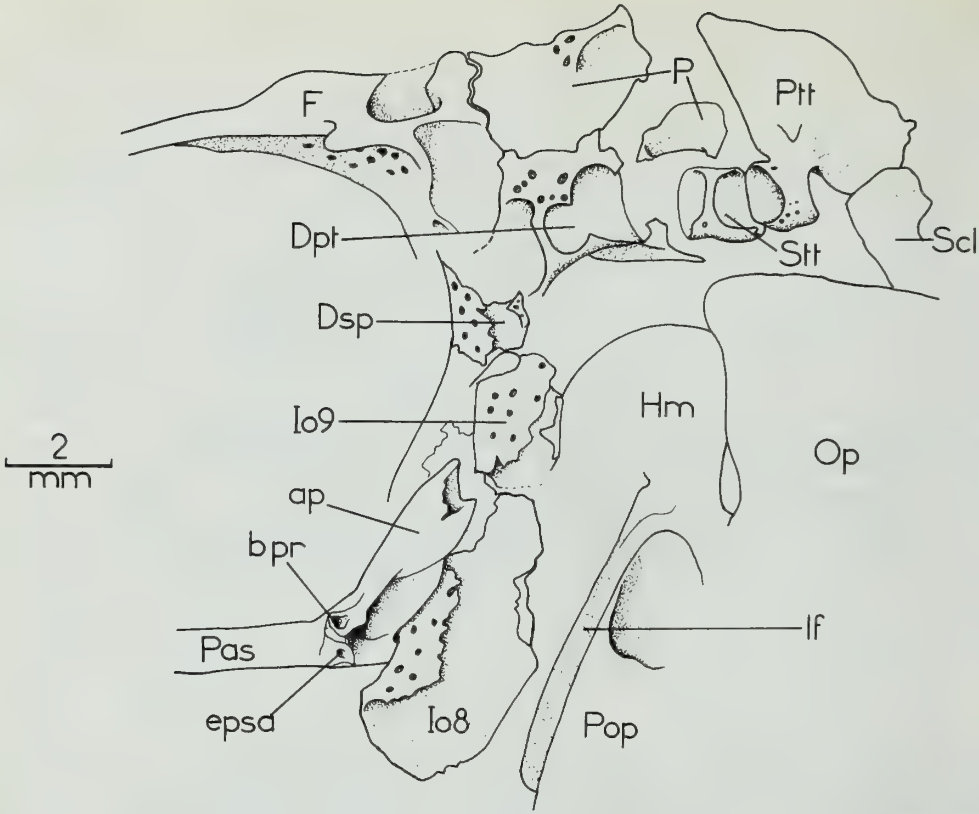

Fig. 5 *Macrosemius rostratus* Agassiz. Postorbital region of left side of skull, as preserved in 37094.

The epioccipital of *Macrosemius* also displays an unusual feature. The dorsal surface of the bone forms a shallow gutter whose relationship with the other cranial cavities is unclear; no such structure has been reported elsewhere. No supraoccipital is present in the specimen; this may be due to faulty preservation.

Patterson (1975 : 454) has suggested that the bone hitherto considered to be the epioccipital in *Lepisosteus* and *Lepidotes* may be the pterotic, the former having been lost. This is not the case in *Macrosemius*, however, where a small part of the pterotic is visible between the prootic and the skull roof. A small part of the sphenotic is also visible above the prootic, underlying the dermosphenotic.

The ventral half of the prootic, which formed the walls of the otolith chamber and the myodome, is not preserved. The posterior edge of the bone forms a stout flange which housed the ampulla of the horizontal semicircular canal, as in *Lepisosteus*. The inner surface of the prootic, immediately anterior to this flange, forms a recess presumably for the utriculus. Below this recess the bone becomes very thin; the region of the suture with the basioccipital is lost in the specimen. Part of the pterosphenoid, revealing its smooth medial surface, is also preserved.

The orbitosphenoid (Fig. 13) is preserved in AS.1.770. The bone lies unusually far forward between the frontal and the parasphenoid. The posterior edge forms several shallow embayments. Saint-Seine (1949 : fig. 88–89a) found a similar orbitosphenoid in *M. fourneti*.

Part of the preorbital region of the braincase is exposed in 37051. A long, stout ossification underlies the frontal and the nasal process of the premaxilla (Fig. 8b). It is not clear whether this dorsal ethmoid ossification is median or paired. No other ossifications of the snout region of the braincase are preserved.

(iii) Circumorbital bones. No supraorbitals are preserved in the available specimens of *M. rostratus*. Saint-Seine (1949 : 202) has reported their presence in *M. fourneti*. The infraorbital series comprises 11 bones: antorbital, nine infraorbitals and dermosphenotic. These are visible in 37051 and 37094.

The antorbital forms a long, gradually tapering tube around the anterior part of the infraorbital sensory canal. The canal was exposed by two large fenestrae which pierce the posterior part of the tube; two smaller openings occur in the narrow anterior part which curves medially across the premaxilla.

The first three infraorbitals (Fig. 4) cover the lateral surface of the maxilla when this is raised. They are thin sheets of bone whose upper margins curled over the dorsal surface of the infraorbital sensory canal. The following four infraorbitals lie below the orbit, and differ from the first three in lacking the ventral extension. The eighth and ninth infraorbitals lie behind the orbit (Fig. 5); both form complete tubes around the sensory canal, and the eighth is about twice the length of the ninth. The walls of the tubes are perforated by small holes.

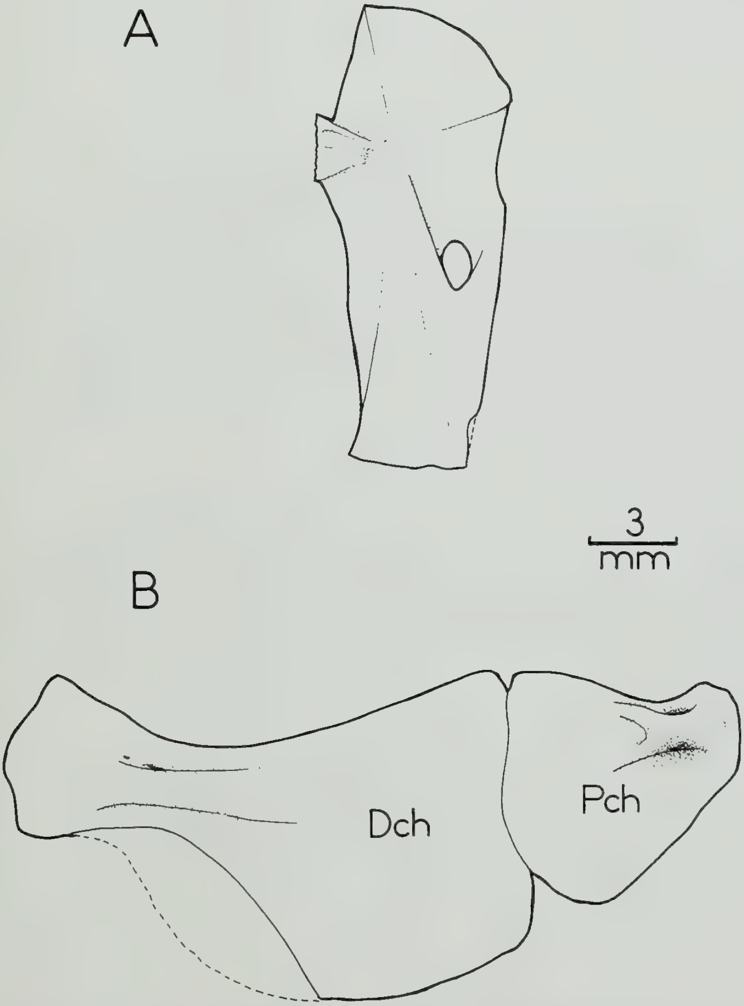

Fig. 6 *Macrosemius rostratus* Agassiz. A, isolated left hyomandibular in medial view. B, isolated right ceratohyal in medial view. AS.1.640.

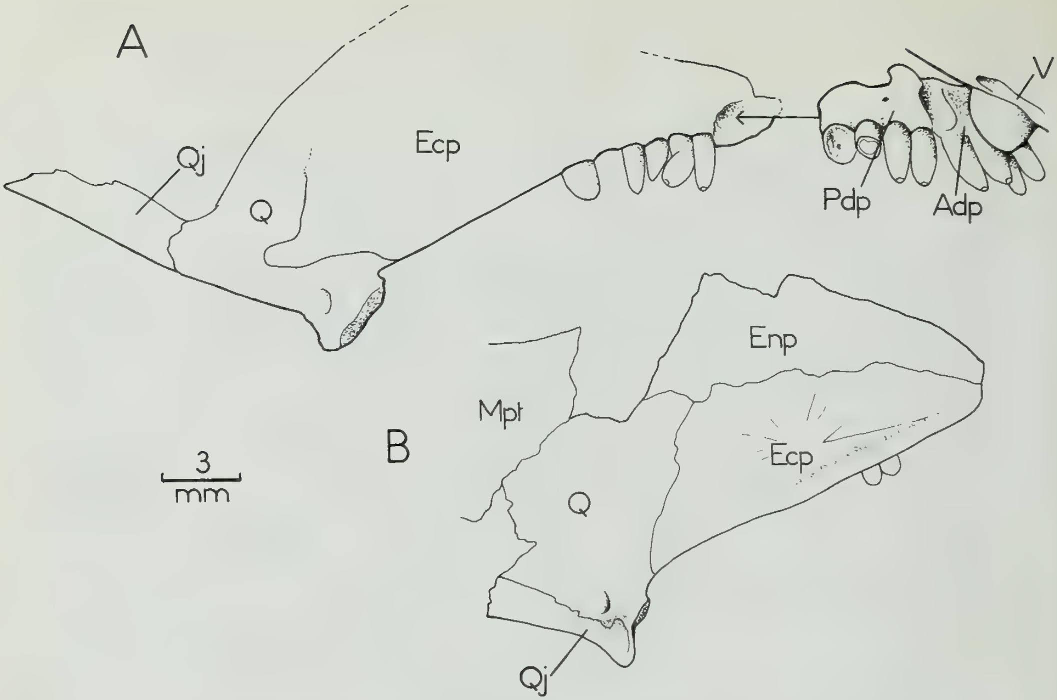

Fig. 7 *Macrosemius rostratus* Agassiz. Two views of the palate. A, medial view with palatines displaced forward, AS.1.770. B, lateral view, AS.1.640.

The dermosphenotic resembles the last two infraorbitals in forming a short, vertical, perforated tube around the sensory canal. The anterior wall of the tube extends along the orbital wall of the frontal, to which it was probably fixed. Thus, although not hinged to the skull roof as it is in *Lepisosteus*, the dermosphenotic of *Macrosemius* is not fully incorporated into the roof as in *Amia* but retains the characteristics of an infraorbital.

As in all other members of the Macrosemiidae, suborbitals are absent.

(iv) Hyopalatine bones. The hyomandibular is preserved in medial view in AS.1.640. The proximal articulatory facet forms a quadrant facing anterodorsally. The short, stout opercular process occurs about one-third of the way along the posterior edge from the proximal end (Fig. 6A). The foramen for the hyomandibular nerve pierces the bone close to the anterior edge, slightly below the mid-point along the length of the bone. The lateral surface of the hyomandibular (37051; Fig. 5) bears a narrow, anteriorly-inclined flange alongside the leading edge of the preopercular, forming an elongated recess.

The metapterygoid is not clearly exposed in any of the specimens. Its form approximates to that of a disc lacking a large anterodorsal segment; the two straight edges form an obtuse angle (Fig. 11). The upper, dorsally-inclined edge articulated with the basipterygoid process.

The remainder of the palate is preserved in medial view in AS.1.770, and in lateral view in AS.1.640 (Fig. 7). The quadrate is roughly triangular, with a convex posterodorsal edge which extends to the metapterygoid in older specimens. The articulatory facet on the quadrate is very broad and faces forward. The posteroventral edge of the quadrate is closely applied to an elongated bone of dermal origin which lies along the dorsal surface of the ventral arm of the preopercular. This elongated bone is covered by the quadrate along the anterior half of its medial surface. Its distal end is expanded and fits closely against the posterior surface of the thin lateral part of the quadrate condyle; fusion occurs between the two elements in this region. A bone of similar form and relationship with the preopercular and quadrate has been described by Patterson (1973 : fig. 26) in *Lepidotes* and *Dapedium* and identified by him as the quadratojugal.

The ectopterygoid has a complicated overlapping suture with the quadrate, which occupies only a very small length of the lateral border of the palate. The lateral border of the ectopterygoid bears a row of about six stout teeth, increasing in height anteriorly; the medial border forms a long straight suture with the endopterygoid. The endopterygoid bears no teeth.

Two dermopalatines precede the ectopterygoid; each bears four stout teeth, similar in size and form to those on the ectopterygoid.

(v) Dermal upper jaw. The premaxilla has a broad dentigerous head, produced dorsoposteriorly to form a slender nasal process. The premaxillary teeth form a transverse row of four or five; they are stout, laterally compressed and taper to a blunt point (Fig. 8). The slender, tapering nasal process sutures with the dorsal ethmoid ossification, beneath the nasal. The medial surface of the process is expanded to form a short, narrow gutter along which lay the olfactory nerve. A small foramen pierces the base of the nasal process close to the medial edge; this presumably transmitted the anterior palatine ramus of the facial nerve. A similar condition is found in *Amia* (Allis 1897 : pl. 21).

Anteriorly the maxilla forms a long, stout, cylindrical medial process which rotated in the space between the vomer and premaxilla (Fig. 8). The upper and lower edges of the maxillary expansion are approximately straight and parallel to each other; the posterior border is convex. The dorsal edge is incised by a deep, anteriorly-directed notch, about midway along its length. The oral border of the maxilla bears about eight sharply-pointed teeth, about half the size of those on the premaxilla (Fig. 4).

As in all other members of the family, the supramaxilla is absent.

(vi) Lower jaw. The short, anterior, dentigerous portion of the mandible is followed by a high coronoid process. The ventral border is markedly concave. Dentary, angular, surangular, prearticular, one coronoid, articular and retroarticular bones are present.

The lower jaw is exposed in medial view in AS.1.770 (Fig. 9). The articular facet is shallow, very broad, and faces posteriorly. Only the lower part of the broad coronoid process of the articular is preserved. A large retroarticular, formed partly of dermal bone, caps the posterior end of the angular, below the articular facet. The retroarticular does not form part of this facet.

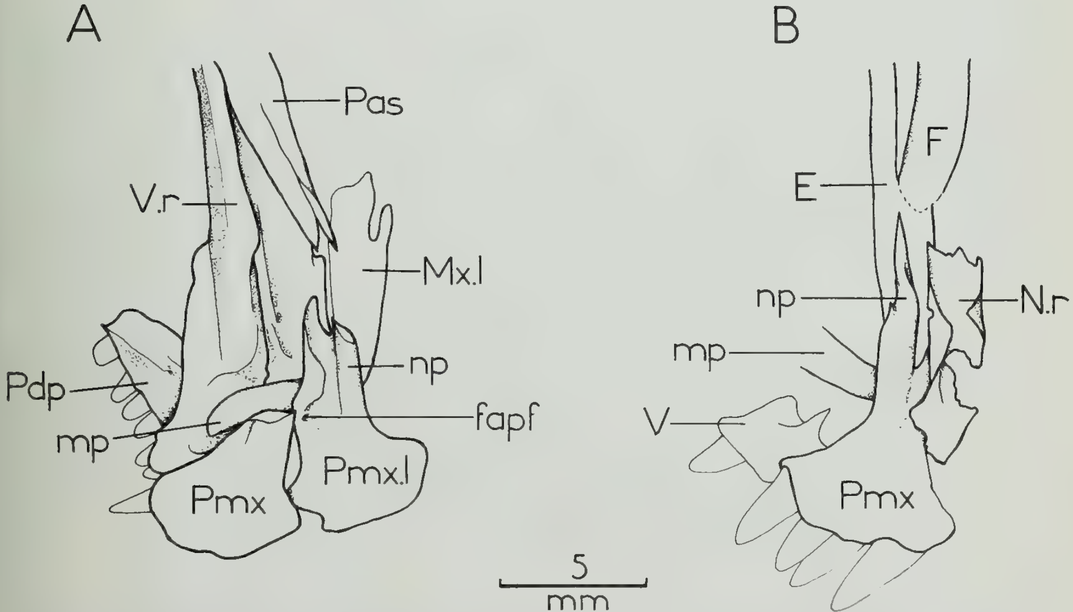

Fig. 8 *Macrosemius rostratus* Agassiz. Two dorsolateral views of the snout region. A, AS.1.640. B, 37051.

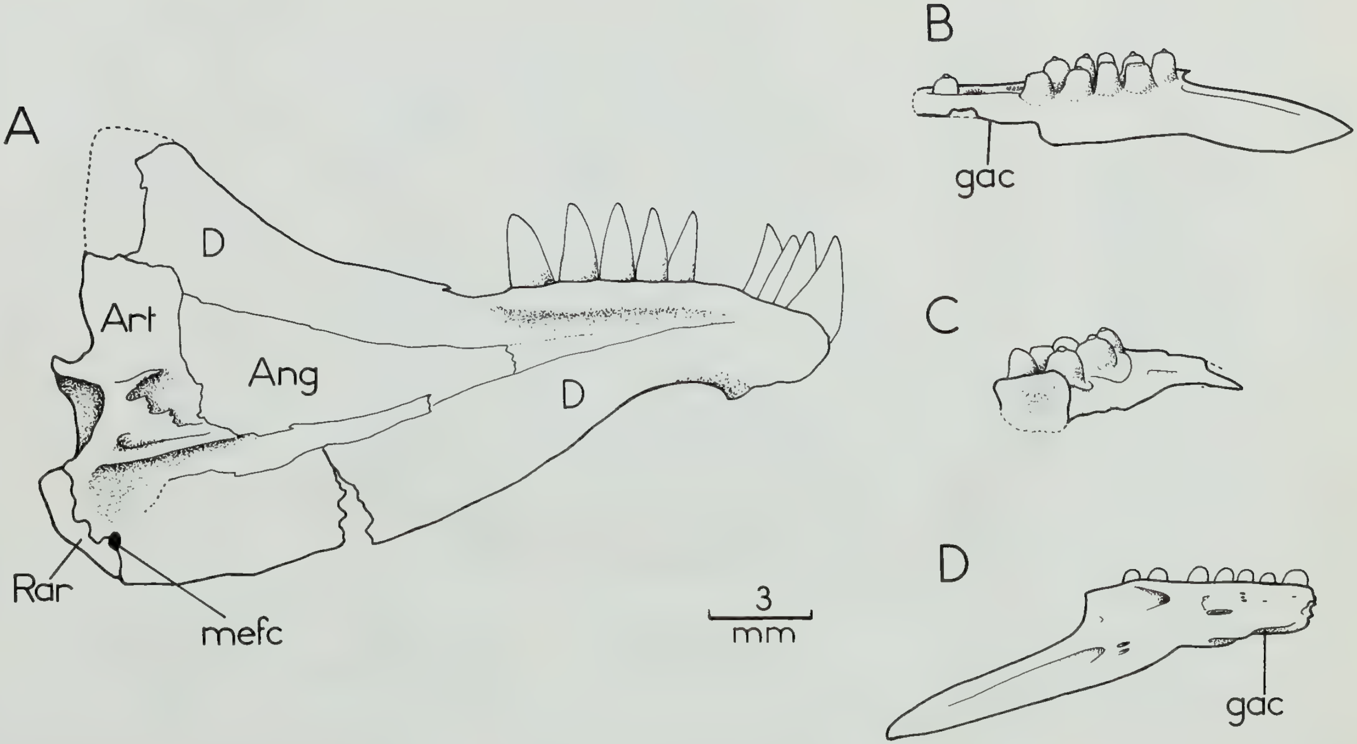
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Fig. 9 *Macrosemius rostratus* Agassiz. Lower jaw. A, left mandible in medial view. B, right prearticular in medial view. C, right coronoid in medial view. All AS.1.770. D, right prearticular in lateral view, AS.1.639.

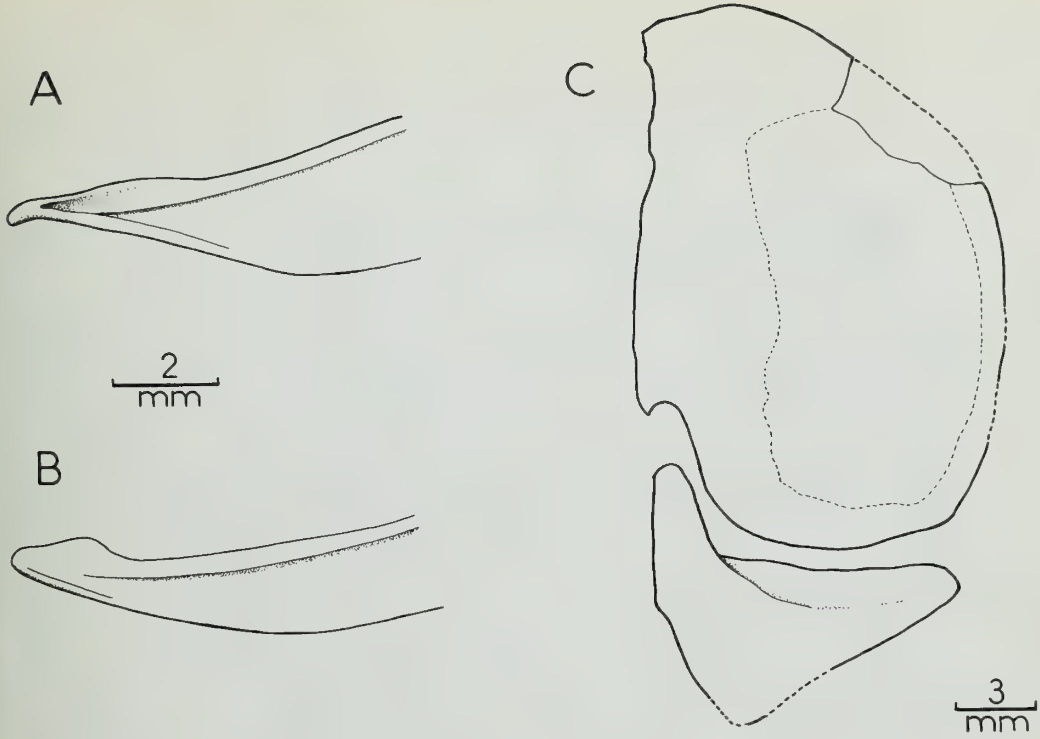


Fig. 10 *Macrosemius rostratus* Agassiz. Lateral views of proximal parts of A, last branchiostegal and B, penultimate branchiostegal in 37094. C, opercular and subopercular of AS.1.640 in lateral view.

The sinuous suture between angular and retroarticular is interrupted by a canal which presumably transmitted the external mandibular ramus of the facial nerve. *Amia* has a similar foramen (Allis 1897 : pl. 20, fig. 6).

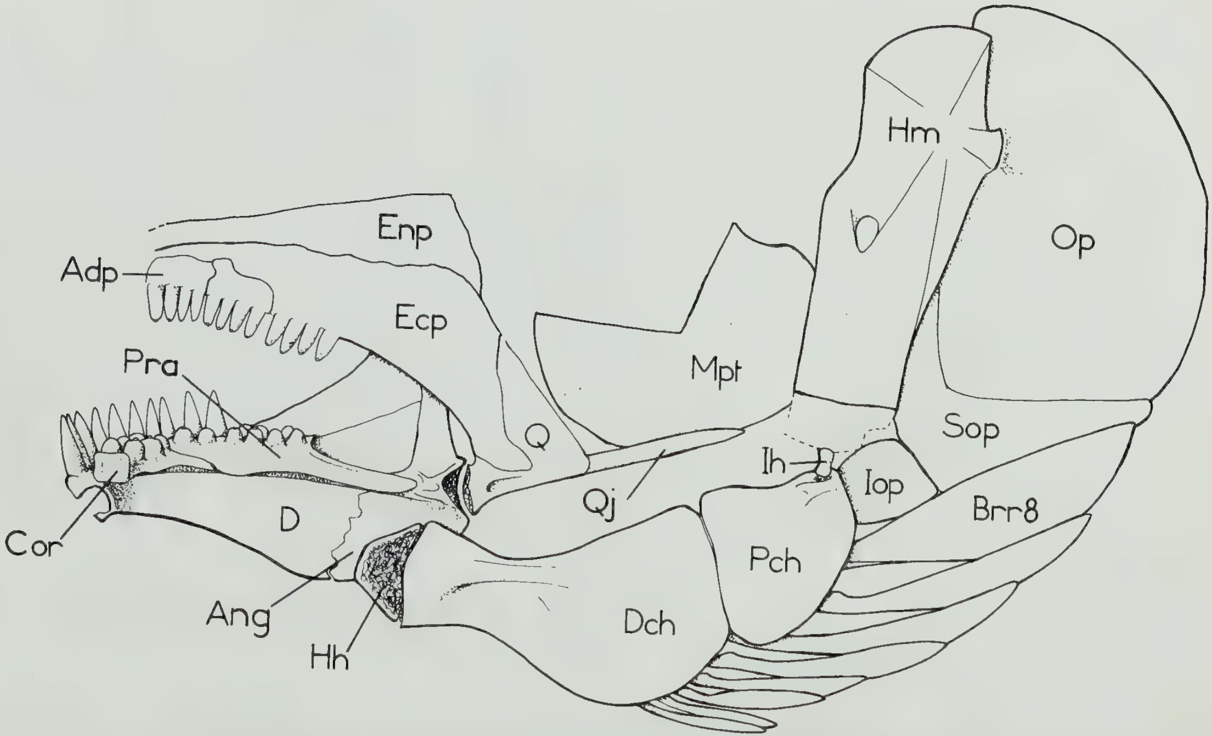
The dentary bears about 10 large teeth. Each tooth is laterally compressed and tapers to a point. The teeth are most closely set in the anterior region where the dentary curves sharply towards the mental symphysis. The lateral surface of the dentary is exposed in 37051 (Fig. 4) and 37094. The oral border of the bone rises steeply and forms the greater part of the dermal coronoid process. The open trough for the mandibular sensory canal is very wide and occupies about half of the depth of the dentary below the tooth-row. Three small indentations on the dorsal and ventral margins of the trough may be the remnants of resorbed arches of bone which spanned the canal at an earlier stage of development.

The small surangular occupies the upper posterior part of the coronoid process.

The mandibular sensory canal continued along a large trough in the ventral part of the angular before turning dorsally beneath the quadrate articulation past the remains of another arch of bone. The angular forms a long tapering extension above the sensory canal in the dentary and forms an interdigitating suture with this bone in the medial wall of the canal trough.

The coronoid and prearticular are preserved displaced from the remainder of the mandible in AS.1.639 and AS.1.770 (Fig. 9). The coronoid is short and bears six mammiliform teeth each with a nipple of ganoine. The surfaces of several of these teeth have been worn flat. The two medial teeth, in opposition to the pair of large vomerine teeth, are larger than those forming the outer row. The ventrolateral surface of the coronoid is produced posteriorly to form a short, laterally-compressed process which fitted beneath the dentigerous part of the prearticular.

The prearticular is about twice the length of the coronoid. The dentigerous portion supports about 11 teeth similar in size and shape to those forming the outer row on the coronoid. The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Pch
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Dch
Hh

Fig. 11 *Macrosemius rostratus* Agassiz. Restoration of right palate, lower jaw and operculum in medial view. × 3 approx.

anterior two or three teeth form a single row; the remainder form two rows. The ventral surface is grooved for the reception of the posterior process of the coronoid. The prearticular itself forms a long blade-like process posteriorly, inclined slightly ventrally. The ventral surfaces and posterior processes of the two bones rested on the thickened ridge on the inner surface of the dentary. Part of the adductor mandibulae muscle presumably passed into the narrow gap between the dentary and the blade of the prearticular and inserted upon this ridge.

(vii) Preopercular, hyoid arch and branchiostegal series. The preopercular is sharply bent below the level of the orbit; the dorsal and ventral arms form an angle of about 135 degrees. The dorsal arm ends at the level of the opercular process of the hyomandibular and does not reach the skull roof. Its medial surface is closely applied to the hyomandibular (Fig. 13). In contrast to the straight leading edge, the posterior border of the dorsal arm is gently convex. The wide, laterally-compressed sensory canal entered the preopercular dorsally, through a large aperture occupying most of the width of the bone. Within the dorsal arm the canal was exposed by three wide fenestrae. The canal was exposed along its ventral surface along the entire length of the ventral arm. In this region the lateral wall of the canal is deeper than the medial wall.

The opercular (Fig. 10) is deeper than broad. Its trailing edge increases in curvature dorsally. The articulation with the hyomandibular occurs at about one-third of its depth from the dorsal edge. Numerous flat, discrete tubercles of ganoine ornament most of the lateral surface of the opercular. The subopercular is small in comparison with the opercular. Its anterior edge forms an ascending process which abuts against a notch in the latter. Most of the dorsal margin of the subopercular is overlapped laterally by the opercular. A few tubercles of ganoine ornament the bone.

The interopercular is very small, with its anterior end remote from the lower jaw. It forms a straight suture with the subopercular; the remaining edges are rounded.

There are eight branchiostegals, but in one specimen (37094) the lowermost two rays are fused proximally. The uppermost five or six rays are acinaciform and the lowermost two or three

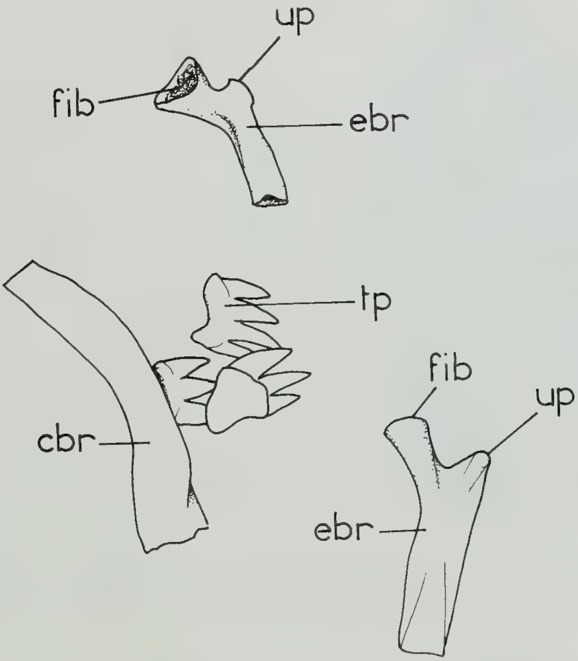

Fig. 12 *Macrosemius rostratus* Agassiz. Scattered parts of the branchial skeleton, as preserved in AS.1.640. × 4 approx.

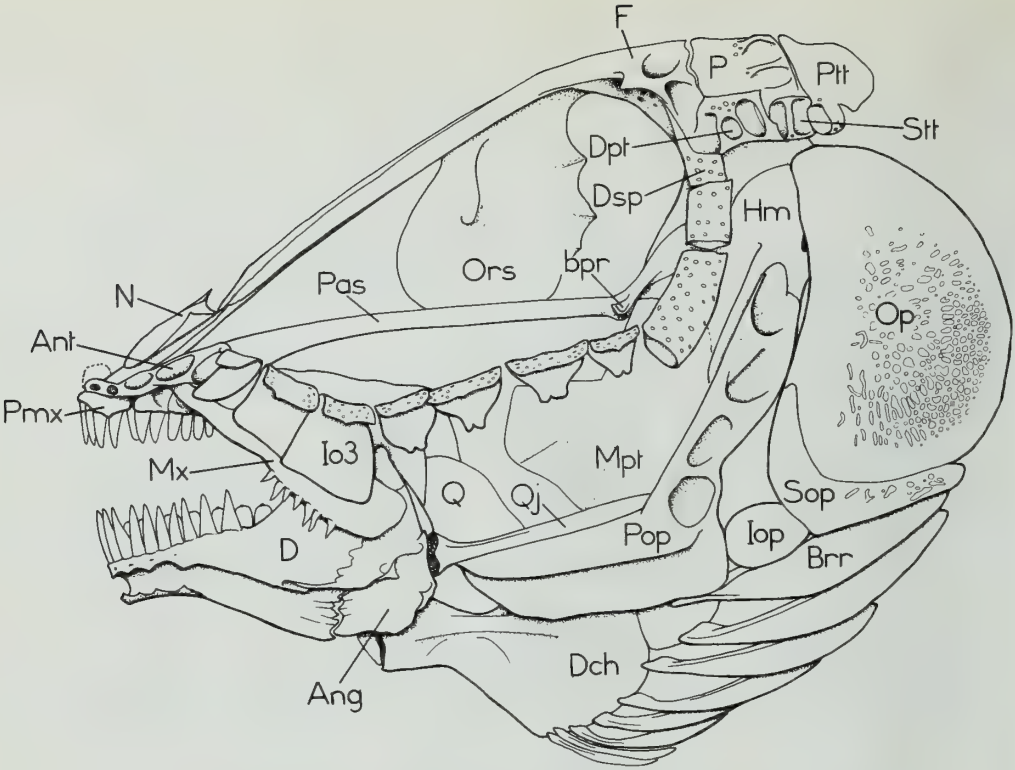

Fig. 13 *Macrosemius rostratus* Agassiz. Restoration of skull. ×2½ approx.

spathiform. The length of the rays decreases rapidly from the top to the bottom of the series. The proximal end of the last (uppermost) ray differs from those of the remainder (Fig. 10); it tapers to a blunt point and is excavated laterally by a deep recess. The dorsal edge of the ray is almost straight. This edge is thickened and curled laterally to form a ventrally-facing groove. This ray does not appear to have articulated with the ceratohyal and was probably fixed to the subopercular. The ventral border of the rays is gently convex. The articulatory heads of the remaining rays form a small dorsal expansion from the thickened upper edge; there is no lateral recess (Fig. 10). The blade of each branchiostegal overlaps that of its ventral successor.

The hyomandibular is described above, together with the palate. The interhyal is very short; it articulated ventrally with a shallow facet close to the posterodorsal corner of the posterior ceratohyal (Figs 6, 11). The distal ceratohyal ossification is short, of little more than twice the length of the posterior ossification, and extends forward to the level of the hind end of the maxilla. The anterior end is slightly expanded and composed of cancellous endochondral bone. Posteriorly the distal ceratohyal forms a very deep, laterally-compressed expansion which articulated with the heads of the branchiostegals. The form of the single hypohyal is not clearly displayed in the specimens.

(viii) Branchial arches. Two epibranchials and a ceratobranchial are preserved, scattered, in specimen AS.1.640 (Fig. 12). The epibranchials are short and slightly bent at about one-third of their length from the articulation with the pharyngobranchial. A short, dorsally-directed uncinate process is also formed at this point.

The ceratobranchial is the usual long, slightly-curved bone. Three small tooth-plates are associated with it, each bearing three or four stout pointed teeth.

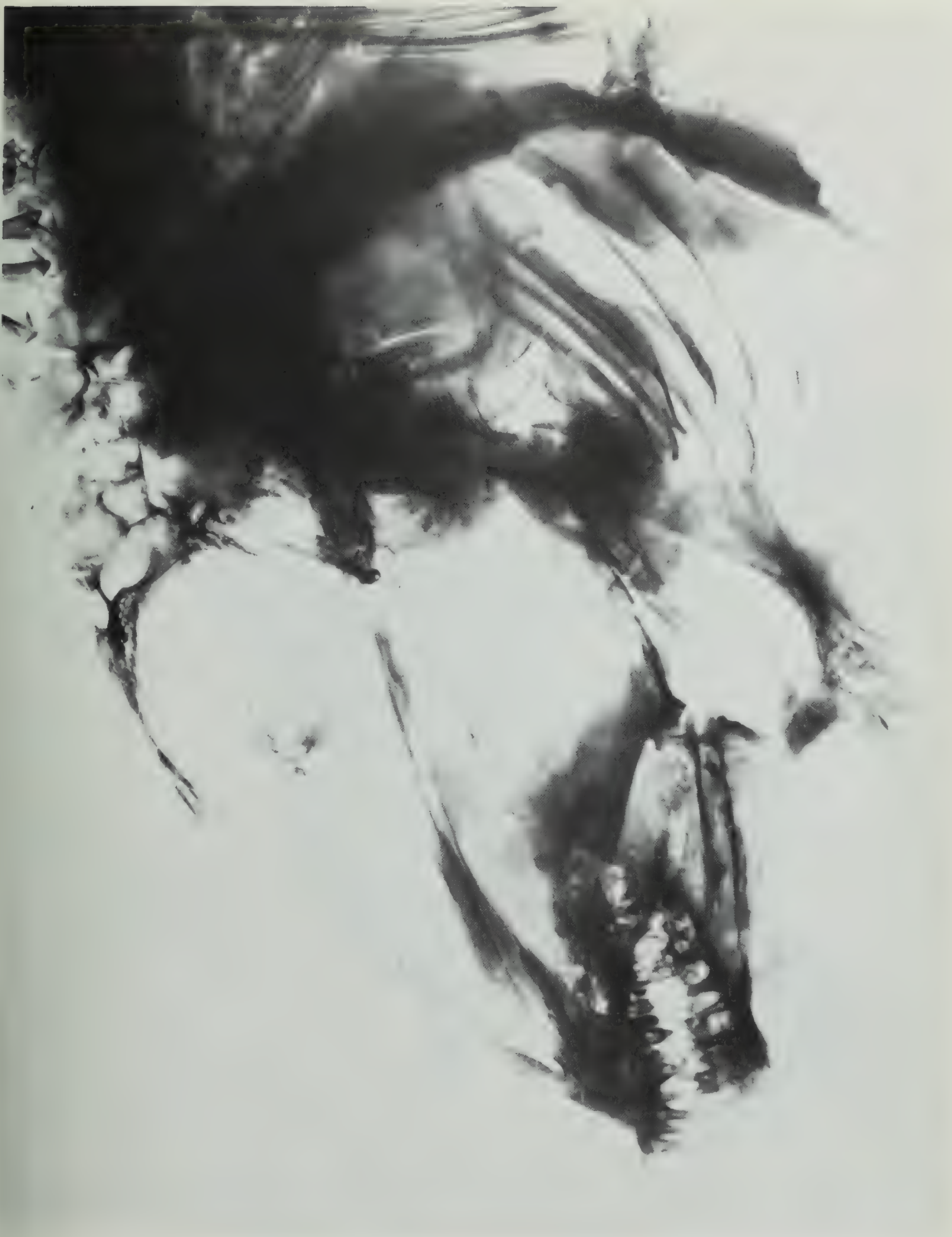

Plate 1 *Macrosemius rostratus* Agassiz. Positive print of a radiograph of the skull and pectoral girdle, transfer preparation of 37094. × 3·375.

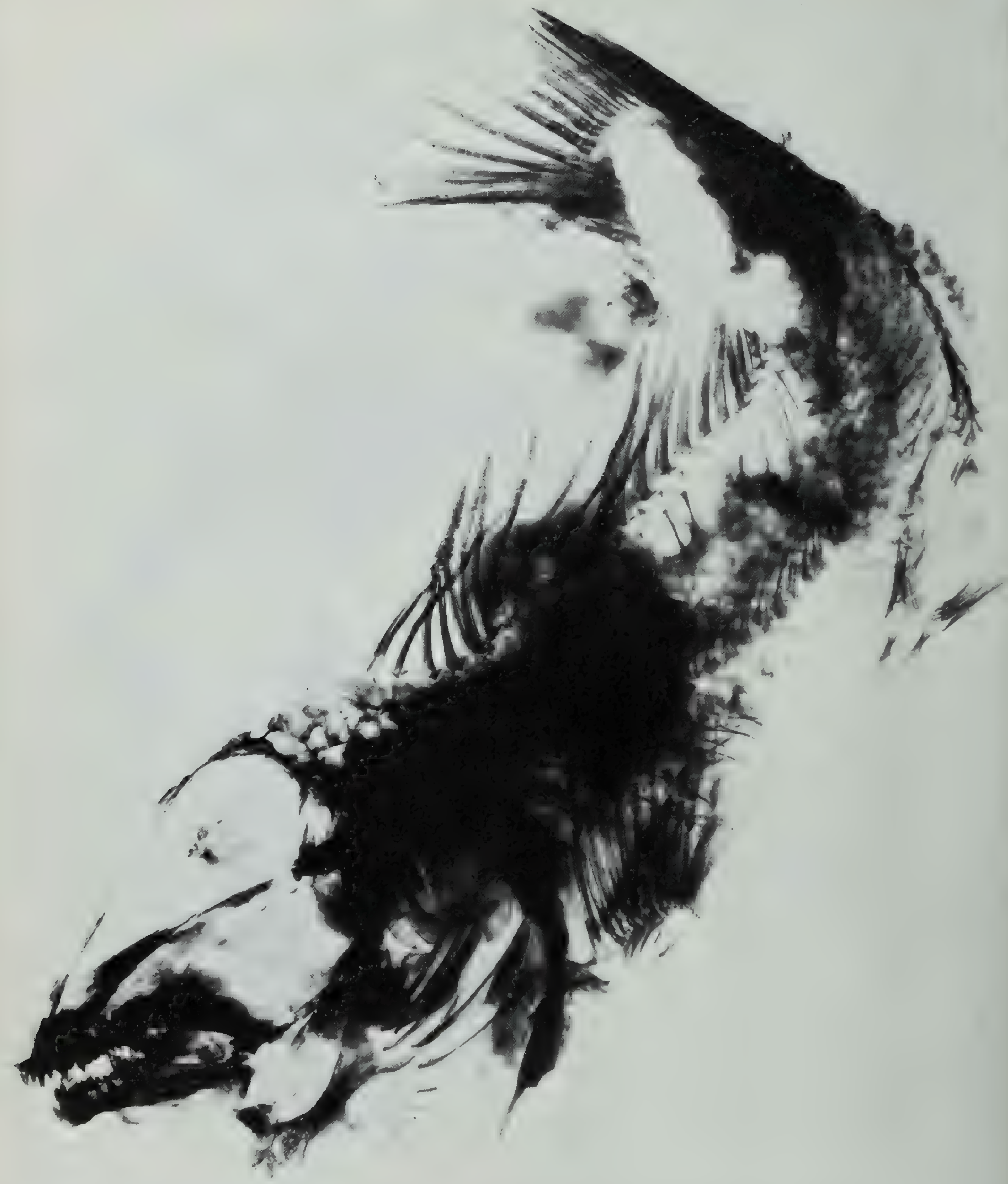

Plate 2 *Macrosemius rostratus* Agassiz. Positive print of a radiograph, transfer preparation of 37094. × 1·65.

(ix) Vertebral column. Several scattered trunk vertebrae are preserved in AS.1.770. The centra are thick cylinders of bone which constricted the notochord and bear three longitudinal ridges on each lateral surface, defining two deep recesses. The lowermost ridge is continuous with a stout, posteroventrally-directed parapophysis (Fig. 14). It is not clear whether the centrum is entirely perichordal in origin or whether a chordacentral component is also present.

The vertebrae in the posterior part of the body remain unknown, except that paired neural spines are visible at least as far back as the level of the anal fin in a radiograph of 37094 (Pl. 2).

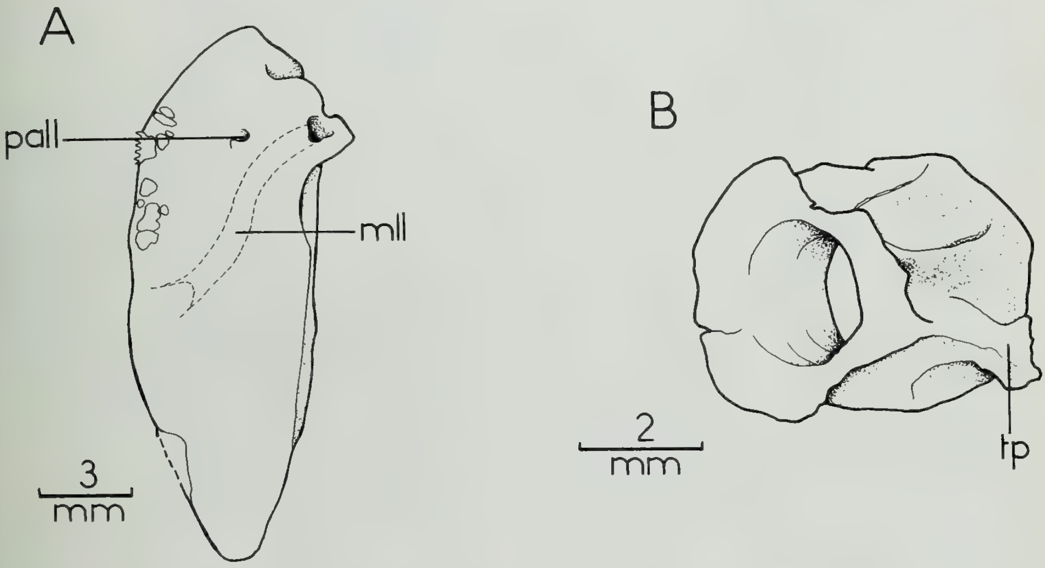

Fig. 14 *Macrosemius rostratus* Agassiz. A, right supracleithrum in lateral view, AS.1.640. **B**, trunk vertebra in anterolateral view, AS.1.770

(x) Pectoral girdle and fin. The left post-temporal is preserved in 37094 (Fig. 5). The triangular laminar portion of the bone tapers towards the midline and is thickened on its ventral surface by a transverse ridge. The lateral margin is inflated to form a short, wide tube around the cephalic part of the main lateral line.

The medial face of the supracleithrum (AS.1.640, Fig. 14) is pierced by the canal of the main lateral line midway along its length. The canal followed an upward sigmoid path through the supracleithrum and emerged through the dorsal part of the leading edge of the bone. The lateral surface bears a pit for a sensory organ posterior to the exit of the sensory canal. A few irregular patches of ganoine occur close to the posterior margin of the supracleithrum; one patch forms serrations along a short length of the margin. The lower part of the bone tapers and overlaps the outer surface of the upper end of the cleithrum.

The cleithrum is preserved in lateral view in AS.1.640 and 37094. The short ventral arm of the bone is inclined downwards forming a wide angle with the dorsal arm. The broad dorsal arm tapers to a point; the lateral surface is shaped to receive the overlap of the supracleithrum. A single vertical row of denticles, each forming three rearwardly-projecting points, extends along the dorsal arm. The lower part of the ventral arm, against which the branchiostegal membrane closed, forms a lateral convexity. The endoskeletal pectoral girdle is not displayed in any of the specimens.

The pectoral fin was supported by about 16 rays associated with six proximal radials (Fig. 15); the cartilaginous distal radials have not been preserved. The first ray is reduced to an unpaired spine. The base of the spine is produced into two lateral, tapering processes for the insertion of the marginal muscle (*sensu* Jessen 1972). The anterior faces of the spine and of the succeeding hemitrich bases are pierced by small, presumably vascular, foramina.

The six proximal radials increase in length posteriorly, with the exception of the fifth, which equals the third in length in 37094. Each radial forms a stout shaft widening slightly towards the extremities. The third and fourth radials are slightly bent in the central region while the same region in the sixth radial bears narrow lateral flanges.

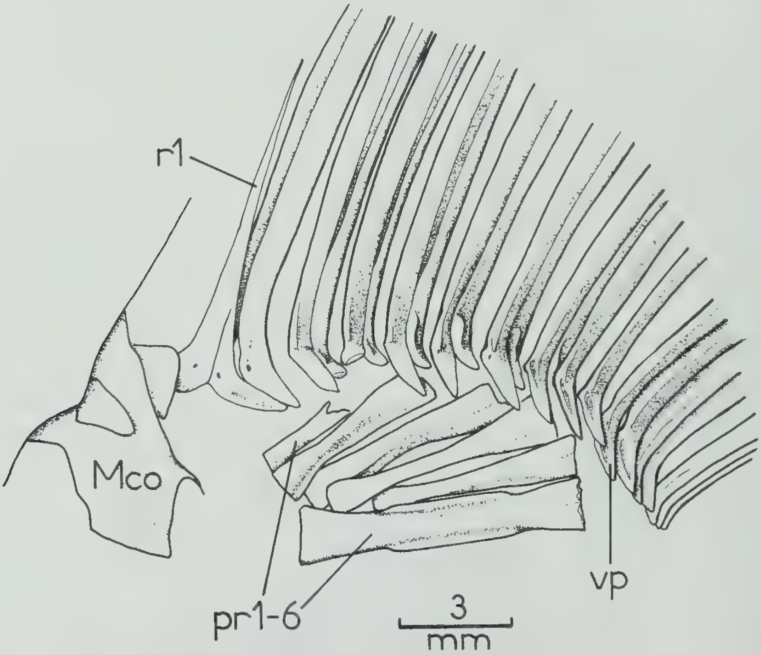

Fig. 15 *Macrosemius rostratus* Agassiz. Base of left pectoral fin in ventral view, as preserved in 37094.

(xi) Pelvic fin. The basipterygium resembles that of *Amia* (Fig. 16). The wide, dorsoventrally-compressed anterior expansion tapers gradually backwards, expanding sharply to form the articular surface. The radials are not exposed in the specimens. The pelvic fin consists of six rays. The base of the leading ray is preceded by four very small splints of bone, the larger two forming a pair. These splints are probably reduced basal fulcra. All the pelvic rays except the first are segmented and branched. The bases of the ventral hemitrichia are produced laterally to form processes for the insertion of the fin inclinator muscles; the length of these processes decreases posteriorly.

(xii) Anal and dorsal fins. The anal fin is large and rounded, with the rays widely spaced and approximately parallel. There are seven rays, each articulating with a long slender radial (37094, Fig. 17). Each hemitrich forms a lateral process at its base for the insertion of the inclinator muscles, as is usual. The leading, unbranched ray is shorter than the unsegmented proximal region of the second ray. The leading ray is preceded by a long, unpaired, asymmetrical splint, and by a pair of shorter splints.

The number of dorsal fin-rays varies between 32 and 39; the dorsal fin-ray counts of six specimens are as follows. 4453 : 32; 1901.67.1 : 38; AS.6.24 : 39; 1954.1.530 : 32; 1904.1.18 : 38; Ei : 37; Ei : 39. The fin extends from the rear of the skull to the base of the axial lobe of the caudal fin. The endoskeletal supports equal the rays in number. Two or three closely-set splints lie in front of the leading ray; these are reduced basal fulcra. No fringing fulcra are present. All the rays branch at least twice; those in the posterior third of the fin branch three times. The fin-rays

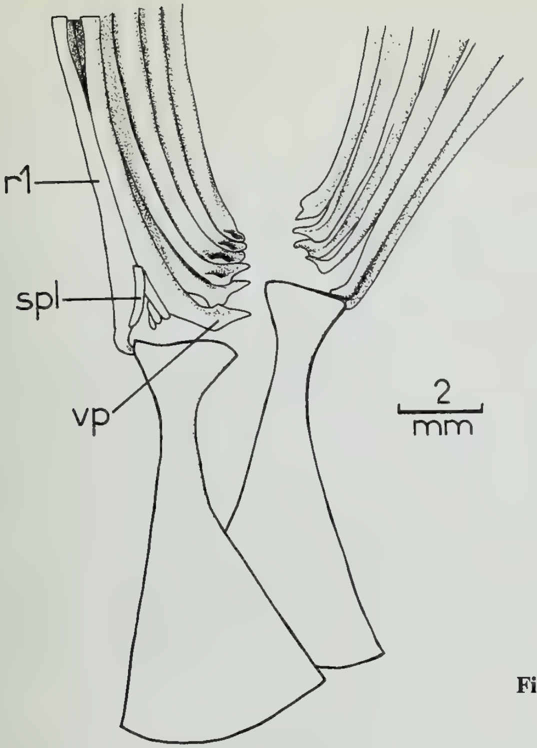

Fig. 16 *Macrosemius rostratus* Agassiz. Pelvic fins and girdles in ventral view, as preserved in 37094.

thicken in lateral profile in the caudal region, where the rays become more closely-set. The dorsal and caudal fin-rays display an unusual feature: the segments of each ray bear one short, dorsally-inclined ganoine spine along the posterolateral surface (Fig. 18); these spines continue onto the unsegmented ray bases.

The distal radials of the fin were presumably of cartilage and are not preserved. Each middle radial segment is inclined backwards (Fig. 18); it is preserved as a thin-walled tube of perichondral bone, irregularly constricted in the centre and pierced by a vascular foramen. The proximal segment is dagger-shaped and flares dorsally to form a thin-walled cone which bore the articulatory surface for the middle segment. A thin flange extends along the lateral surfaces of the proximal radial segment, separating the areas of origin of the elevator and depressor ray muscles. A vascular foramen pierces the base of the cone anterior to the flange.

As usual the radials are arranged so that each ray articulated with both the distal segment of its own radial and with the proximal segment of the succeeding radial.

(xiii) Caudal fin. The number of caudal fin-rays varies between 11 and 13, of which eight originate beneath the axial lobe. The caudal axial skeleton remains unknown. The uppermost ray, supporting a series of fringing fulcra, forms a continuation of the longest axial lobe scale-row, with no sharp demarcation between the two; the base of this ray does not penetrate beneath the squamation (Fig. 19). The remaining axial lobe rays pass beneath the scales and clasp the upper hypurals. The bases of the eight rays originating below the axial lobe clasp only the tips of their endoskeletal supports. The caudal fin is rounded, and only about one-third of its area is supported by the axial lobe rays.

The ventral surface of the caudal peduncle bears four massive basal fulcra, their edges straight and converging to a sharp point. The series is continued along the lowermost fin-ray by paired fringing fulcra which rapidly decrease in size towards the rear of the fin.

(xiv) Squamation. The squamation of *Macrosemius* diplays two features of special interest. Perhaps most striking is the total absence of scales in a strip lying on either side of the dorsal fin, occupying from one-third to a quarter of the depth of the trunk. The squamation of this genus is further characterized by the presence of secondary scale rows which intervene between the transverse rows of the trunk in the region above the first longitudinal scale row dorsal to the lateral line. This scale-pattern is described in *M. fourneti*, below, in which the arrangement of the scales is more surely known.

Below the lateral line the scales form a regular pattern of rectangles. These have been described in a young individual (P7177) by Schultze (1966 : 275, fig. 30). In the anterior region, ganoine is restricted to the denticles on the trailing edge of the scales. The bony layer is crossed by fine radial markings on the anterior half of each scale, and by concentric lines posteriorly. The ganoine-covered area of the scales increases in the caudal region, forming irregular patches. The abdominal scales of an older specimen are displayed in both lateral and medial view in AS.1.640. Here the ganoine layer is complete except for a narrow strip close to the anterior margin; the surface of the ganoine is smooth. Internally the scales forming the transverse rows are linked by small pegs-and-sockets. The shallow internal rib is inclined slightly in advance of the peg-and-socket. Schultze (1966 : fig. 16b) has drawn a lateral line scale in medial view. The sensory canal entered the anterior border of the scale close to the dorsal edge and continued through a thin-walled tube (collapsed in the specimen) which opens midway across the scale and continues as a narrow groove. A small pore, which presumably transmitted the sensory nerve, pierces the wall of the tube.

Three large circumanal scales are preserved in 37094. The anterior pair, which flanked the anus, are roughly oval in shape. They are followed by a large, median saddle-shaped scale immediately preceding the anal fin. All three scales have rounded edges and are devoid of denticles.

The postcleithral scales are nowhere clearly visible. The uppermost, much deeper than wide, is partially visible in some specimens, for example 37094.

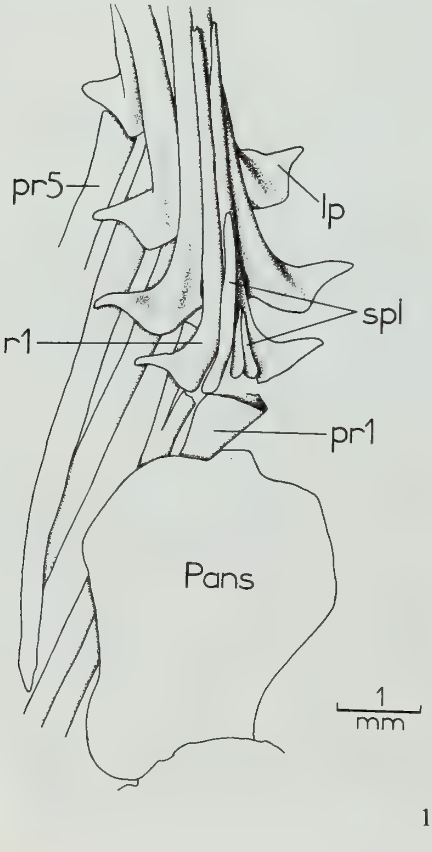

Fig. 17 *Macrosemius rostratus* Agassiz. Base of anal fin in anteroventral view, as preserved in 37094.

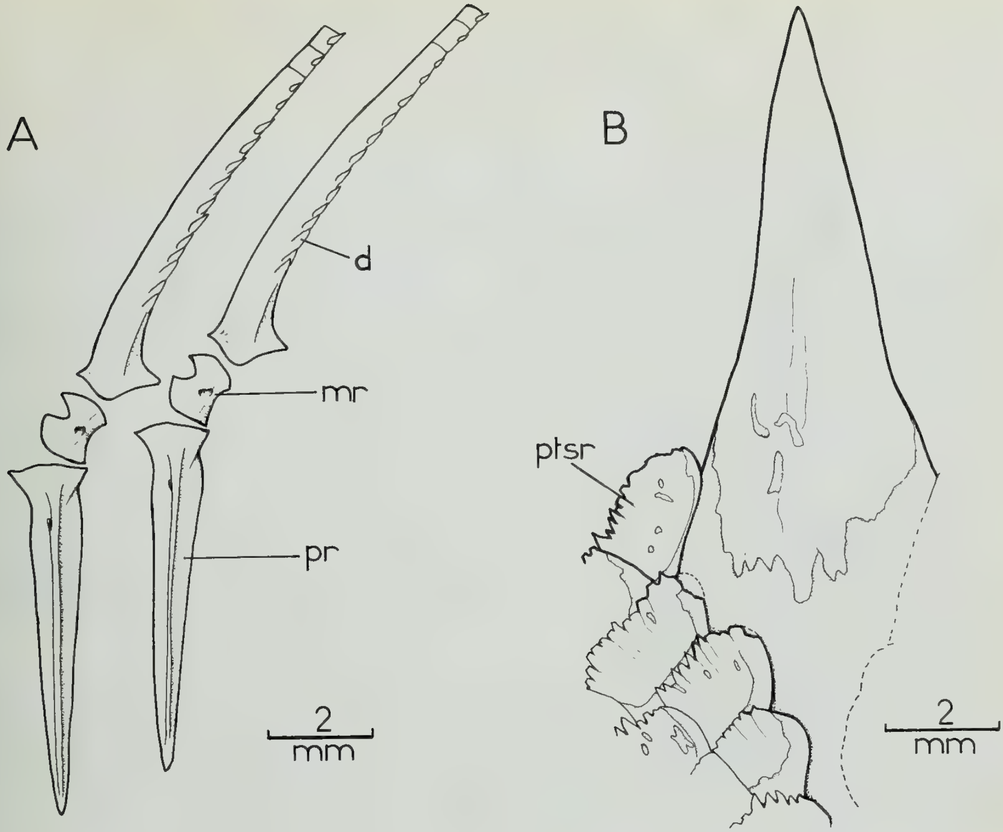

Fig. 18 *Macrosemius rostratus* Agassiz. A, lateral view of two dorsal fin-rays and their supports. B, anterior ventral basal fulcrum on caudal peduncle. 37094.

Macrosemius fourneti (Thiollière 1850)

Fig. 19

1850 *Disticholepis fourneti* Thiollière : 136.
1854 *Disticholepis fourneti* Thiollière; Thiollière : pl. 7.
1858 *Disticholepis dumortieri* Thiollière : 783.
1860 *Disticholepis fourneti* Thiollière; Wagner : 402.
1873 *Disticholepis fourneti* Thiollière; Thiollière : 15.
1873 *Disticholepis dumortieri* Thiollière; Thiollière : 15; pl. 6, fig. 1.
1873 *Macrosemius rostratus* Agassiz; Thiollière : pl. 5, fig. 2.
1883 *Disticholepis dumortieri* Thiollière; Sauvage : 479.
1887 *Macrosemius fourneti* (Thiollière) Zittel : 218.
1895 *Macrosemius fourneti* (Thiollière); Woodward : 178.
1895 *Macrosemius dumortieri* (Thiollière) Woodward : 178.
1914 *Macrosemius fourneti* (Thiollière); Eastman : 365.
1914 *Macrosemius dumortieri* (Thiollière); Eastman : 365.
1949 *Disticholepis fourneti* Thiollière; Saint-Seine : 201; pl. 21a; text-fig. 88–9.
1949 *Disticholepis dumortieri* Thiollière; Saint-Seine : 204; pl. 21b.
1949 *Macrosemius rostratus* Agassiz; Saint-Seine : 199; pl. 23d; text-fig. 87.

DIAGNOSIS. *Macrosemius* with between 33 and 35 dorsal fin-rays, with the mode at 34; the large basal fulcra along the ventral border of the caudal peduncle possessing convex edges; supraorbitals present.

HOLOTYPE. Muséum d'Histoire Naturelle, Lyon, 15.237; from Cerin (Ain, France).

HORIZON AND LOCALITIES. Lower Kimmeridgian of Cerin.

MATERIAL. BM(NH): P1091, P4684–5; specimens in the Muséum d'Histoire Naturelle, Lyon (see Saint-Seine 1949 for registration numbers). None was available for acetic acid preparation.

REMARKS. Thiollière (1858, 1873) and later Saint-Seine (1949) described the following species in their works on the Lower Kimmeridgian fish fauna of Cerin: *Macrosemius rostratus* Agassiz, *Macrosemius helenae* Thiollière, *Disticholepis fourneti* Thiollière and *D. dumortieri* Thiollière. *Disticholepis* strongly resembles *Macrosemius*. However, both authors took *M. helenae* to be typical of the latter genus and considered that the specimens of *Disticholepis* were sufficiently dissimilar to justify the erection of the new genus. *M. helenae* and *Disticholepis* are indeed very different, since in fact the former was wrongly placed in the genus *Macrosemius*. Both Thiollière and Saint-Seine believed that the dorsal fin of *M. helenae* was single; it is, however, divided, and in the present study this species has been transferred to *Notagogus*.

Thus, following Zittel (1887) and Woodward (1895), *Disticholepis* is synonymized with *Macrosemius*. As Saint-Seine (1949 : 404) says, *M. fourneti* and *M. dumortieri* are very similar; they are considered here to be conspecific. The specimens from Cerin hitherto referred to *M. rostratus* are not known in enough detail to be separated from *M. fourneti*.

Saint-Seine's (1949 : 199–204) interpretation of the material of *M. fourneti* is reassessed below by comparison with the type species.

DESCRIPTION. (i) Skull roof and braincase. The drawing given by Saint-Seine (1949 : fig. 87) under the name of *M. rostratus* (15.229) is inaccurate; the bones of the skull roof are crushed and their outlines difficult to discern. There is no evidence that the supraorbital sensory canal followed the course given in the figure.

The skull roof is displayed in lateral view in 15.235 and 15.226; it is very similar to that of *M. rostratus*. Saint-Seine (1949 : 202) discusses several peculiarities of the skull roof. The 'hiatus' he describes between the frontal and parietal is probably due to the post-mortem separation of the non-overlapping suture between the two bones, and was not present in life as he suggests. The fenestrae in the supratemporal commissure, described in *M. rostratus* above, he interprets as 'une rangée de cuvettes très plates separées par des piliers en relief'; he considered these to be distinct

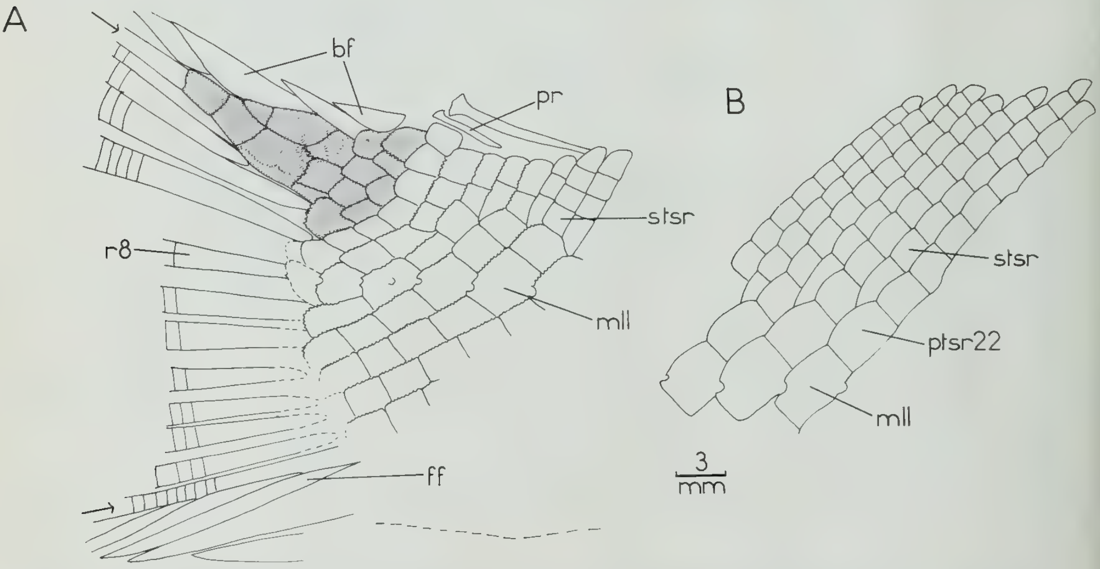

Fig. 19 *Macrosemius fourneti* Thiollière. Squamation, as preserved in impression in P4685. A, caudal region, axial lobe shaded. B, abdominal region, above main lateral line.

from the commissure which he supposed crossed close to the anterior border of the parietal (1949 : fig. 88–89). There is no evidence to support this position for the commissure. Saint-Seine correctly notes the reduced size of the supratemporal. The dermopterotic and frontal too are similar to those of *M. rostratus*.

In contrast to *M. rostratus*, *M. fourneti* has a row of four supraorbitals along the lateral embayments of the frontals (Saint-Seine 1949 : 202).

(ii) The infraorbital series. The dermosphenotic resembles that of the type species. Two of the infraorbitals are identified by Saint-Seine in the preorbital region (1949 : fig. 88–89). The remaining bones of the head are too badly crushed for a useful description to be given. The few structures which are clearly visible resemble those of *M. rostratus*; eight branchiostegals are preserved in 15.289 and the stout rounded teeth of the palatine and splenial bones are visible in 15.226. As in the type species, the opercular is ornamented with discrete tubercles of ganoine (15.226).

(iii) Paired fins. These are exposed in 15.229. As in *M. rostratus* the pectoral fin is preceded by a spine-like ray and the pelvic fin by reduced basal fulcra. Fringing fulcra are absent on both fins.

(iv) Anal and dorsal fins. The anal fin resembles that of the type species. The number of dorsal fin-rays varies between 33 and 35, with the mode at 34. The dorsal fin-ray counts of five specimens are as follows. 15.219 : 34; 15.235 : 34; 15.229 : 33; 15.222 : 34; 15.237 : 35. This contrasts with the larger range of 32–39 displayed by *M. rostratus*. The variation in fin-ray structure along the length of the dorsal fin was noted by Thiollière (1873 : 14). As in the type species the rays in the posterior part of the fin become broader, presenting a larger lateral surface area. Also the unsegmented bases are shorter in the caudal region. The denticles along the fin-rays clearly originate from the tubercles of ganoine on the posterolateral surface of each ray segment.

(v) Squamation. The squamation of the dorsal region of the trunk is clearly discernible in impression in P4685 (Fig. 19). The area along either side of the dorsal fin is completely free from scales. The lateral line scales are the deepest, and number about 40; a few bear pits of the accessory lateral line. As in *M. rostratus*, secondary scale rows occur between the transverse rows. The most anterior of these secondary rows, comprising three or four scales, appears most often behind the twelfth or thirteenth transverse row counting from the head. There follows an interval of several rows before increasingly longer secondary rows interpose between all subsequent rows before the caudal fin. The secondary rows extend ventrally to reach the longitudinal scale row above the lateral line. The scales of the regular transverse rows are narrowed to equal the width of the secondary rows adjacent to them.

The axial lobe of the caudal fin, as defined by the 'reversed' squamation, is small (Fig. 19); this may be correlated with the fact that few (3–5) of the caudal fin-rays originate from the lobe compared with the number of rays which emerge below it (8, as in all macrosemiids). The axial lobe squamation of *Macrosemius* consists of about four disorganized rows; the longest, with about six scales, continues as the hemitrich of the uppermost caudal fin-ray, and the remaining rows terminate dorsally as basal fulcra.

Genus *LEGNONOTUS* Egerton 1854

Diagnosis. Small macrosemiid fishes, the trunk tapering gradually to form a broad caudal peduncle; skull roof bearing ganoine; gape small, the quadrate articulation lying beneath the anterior part of the orbit; dentigerous expansion of maxilla with upper and lower borders straight and diverging posteriorly, hind border also straight and perpendicular to oral border, bearing about 13 small, closely-set teeth; mandible with dentary bearing about 12 closely-set teeth, coronoid teeth rounded; leading edge of preopercular forming sharp angle; abdominal vertebrae forming thin cylinders, notochord unconstricted; pectoral fin with about 15 rays, leading ray reduced to unpaired splint, no fringing fulcra; pelvic fin formed by five rays preceded by basal and fringing fulcra; anal fin with seven rays, base compact; caudal fin weakly forked, axial lobe bearing five rays; dorsal fin single and long, preceded by basal and fringing fulcra, outline high anteriorly, convex posteriorly; region immediately on either side of dorsal fin devoid of scales; scales rhomboid.

Type species. *Legnonotus cothamensis* Egerton 1854.

Introduction. The genus *Legnonotus* was founded by Egerton (1854) to include a small fish with an elongated dorsal fin, *L. cothamensis*, from the Rhaetic of Gloucestershire. Later Woodward (catalogue MS) intended to transfer Gorjanovic-Kramberger's (1905) specimens of *Ophiopsis attenuata* Wagner, from the Upper Trias of Hallein (Austria), to a new species of this genus, *L. krambergeri*; this manuscript name is now given formal status. The latter species is described first since it is the better known of the two.

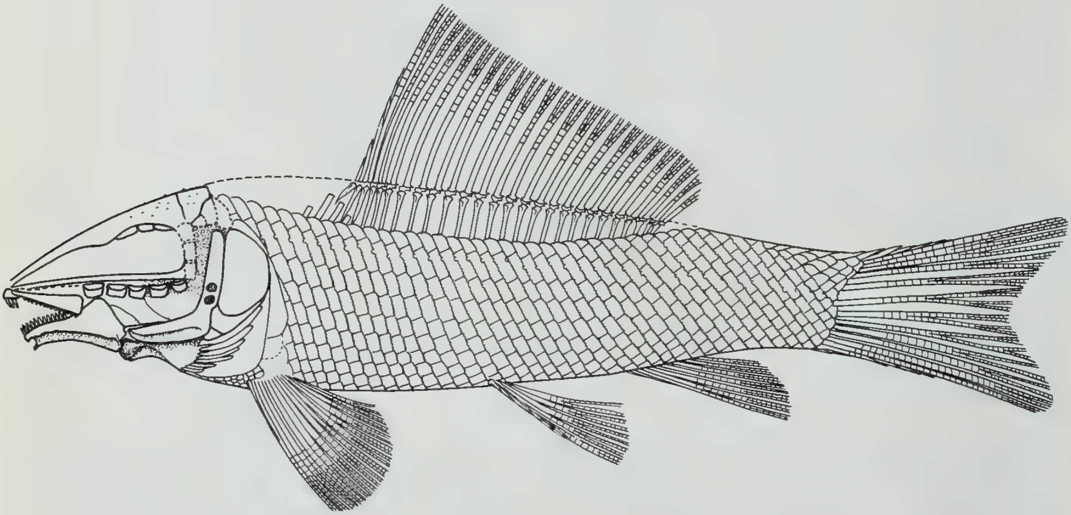

Fig. 20 *Legnonotus krambergeri* sp. nov. Restoration of skeleton. ×2½ approx.

Legnonotus krambergeri sp. nov.

Fig. 20

1905 *Ophiopsis attenuata* Wagner; Gorjanovic-Kramberger : 218; pl. 20, figs 3, 4.

Diagnosis. *Legnonotus* with about 25 dorsal fin-rays; dentary teeth tall and sharp.

Holotype. British Museum (Natural History) P10287, from the Upper Trias of Hallein, Austria.

Horizon and Locality. Upper Trias of Hallein, Austria.

Material. BM(NH): P10287, P10286; Leo: 75, 88, 93, 98, 108.

Remarks. The small jaws, lack of a gular and supramaxilla and the form of the infraorbitals in this genus all indicate that these fishes belong to the Macrosemiidae *s. str.* and not to *Ophiopsis*. They are ascribed to the poorly-known genus *Legnonotus* on account of the long, single dorsal fin and the forked tail.

Description. (i) General features. *Legnonotus krambergeri* is a small elongate fish reaching a standard length of 65 mm (Fig. 20).

(ii) Skull roof and braincase. The skull roof is poorly preserved in the specimens; it is best seen in specimens 93 and 108. The parietals are ornamented with small, regularly dispersed tubercles of ganoine. Their greatest width is along the frontoparietal suture, which is gently convex anteriorly. The lateral border of the parietal is embayed posteriorly where it formed contact with the supratemporal (88). The supratemporal commissure is not visible.

The frontals have the usual macrosemiid form, with a long slender preorbital region and a short, broad postorbital region. As usual, the supraorbital sensory canal runs close to the posterior edge of the orbital embayment before turning medially to pass alongside the straight interfrontal suture. As in *Macrosemius* the canal lay in a trough formed by the frontals in the preorbital region. The ganoine ornament on the posterior part of the frontal is preserved in impression in specimen 88; the ganoine tubercles are aligned in rows parallel to the midline. In 93, the ganoine forms complete ridges. The remaining bones of the skull roof are unknown.

(iii) Circumorbital bones. Three supraorbitals lie in the orbital embayment of the frontal. Their surface is ornamented with a few discrete tubercles of ganoine. Traces of four infraorbitals are visible in specimen 108; these are probably the 4th–7th of the series, and appear to resemble those of the type genus. The dermosphenotic is not preserved.

(iv) Dermal upper jaw. The maxilla is preserved in impression in specimens 93 and 108. The dorsal and oral borders are straight, and diverge posteriorly. The latter bears a long row of about 13 very small teeth. The hind border is also straight, and is perpendicular to the lower.

(v) Lower jaw. The dentary bears a row of about 12 tall, pointed, closely-set teeth. Although the bones of the lower jaw are crushed beyond recognition, enough is visible in specimen 93 to show that, as in other members of the family, the mandibular sensory canal ran in an open groove along the ventral border. The jaw articulation lies below the anterior part of the orbit. Several coronoid teeth, their apices worn flat, are visible in the same specimen.

(vi) Preopercular and opercular series. What little of the preopercular can be seen in the specimens indicates that this bone was sharply bent as in *Macrosemius*. The opercular series is best preserved in specimen 93. The opercular is somewhat wider in proportion to its depth than it is in the type genus. The branchiostegals display a marked reduction in length and depth passing down the series. The distal ceratohyal is preserved in impression in 108; as in other macrosemiids the proximal end is stout, expanding to form a deep, laterally-compressed expansion posteriorly.

(vii) Vertebral column. Abdominal centra are exposed in 93, although they are too poorly preserved for an accurate description to be given. Six supraneurals are visible behind the skull in P10286 and 93, as in *Macrosemius*.

(viii) Pectoral fin. The pectoral fin was supported by about 15 rays preceded by an unpaired spine, probably a modified ray as in the type genus. There are no fringing fulcra.

(ix) Pelvic fin. The pelvic fin consists of five rays; the leading ray is preceded by about four basal fulcra and two pairs of fringing fulcra.

(x) Dorsal and anal fins. The dorsal fin consists of about 25 rays. As in *Macrosemius*, the fin is undivided. The anterior rays are the tallest, the remainder decreasing in height to form a gently concave border. Seven basal fulcra and several pairs of fringing fulcra are present. The radials are similar to those of the type genus.

The anal fin consists of seven rays; their bases are crowded more closely together than those of *Macrosemius*.

(xi) Caudal fin. The outline of the fin is weakly forked. Five rays emanate from the axial lobe and eight, as usual, from below the lobe. Both upper and lower edges bear basal and fringing fulcra.

(xii) Squamation. *Legnonotus* shares with *Macrosemius* the absence of scales along a strip on either side of the dorsal fin. The lateral line, passing through about 37 deep, rhomboid scales, is placed in an unusually high position along the body. Unlike the condition in the type genus, no secondary transverse scale-rows occur.

Legnonotus cothamensis Egerton 1854

1854 *Legnonotus cothamensis* Egerton : 435.
1855 *Legnonotus cothamensis* Egerton; Egerton : 4; pl. 7, figs 9–12.
1895 *Legnonotus cothamensis* Egerton; Woodward : 176.
1966 *Legnonotus cothamensis* Egerton; Schultze : 274, text-fig. 29.

DIAGNOSIS. *Legnonotus* with about 30 dorsal fin-rays; dentary teeth blunt.

HOLOTYPE. Specimen in the Bristol Museum.

HORIZON AND LOCALITY. Rhaetic (Cotham Marble) of Aust Cliff, Gloucestershire, England.

MATERIAL. BM(NH): P1092, three pieces of matrix containing scattered fragments, of which one was prepared in dilute acetic acid.

DESCRIPTION. Unfortunately the bones in the BM(NH) material are largely fragmented. The only bone which can certainly be identified as part of a macrosemiid is a right dentary. The remaining fragments, mainly of scales and vertebrae, may belong to the other fish found in the Cotham Marble, *Pholidophorus higginsi* (Egerton 1855). The centra present consist of rings of dense bone to which the cancellous cartilage-bone of the arches and transverse processes are attached. These are closely similar to the centra of *Ichthyokentema* (Griffith & Patterson 1963) and are unlikely to belong to *Legnonotus*. Similar doubt applies to the identity of the deep trunk scales drawn by Schultze (1966 : fig. 29).

Genus *ENCHELYOLEPIS* Woodward 1918

DIAGNOSIS. Very small macrosemiid fishes, trunk gradually tapering from the occiput backwards; head large; dentary teeth closely set and pointed; abdominal centra annular, neural and haemal arches short and stout; about five pelvic fin-rays; dorsal fin long, undivided, with about 25 rays articulating upon stout radials; seven anal fin-rays; caudal fin rounded; scales cycloid, overlapping.

TYPE SPECIES. *Macrosemius andrewsi* Woodward (1895a).

INTRODUCTION. Sauvage (1883) described a very small macrosemiid from the Upper Portlandian of Meuse (France), *Macrosemius pectoralis*. Woodward (1895a) described another similar species, *M. andrewsi*, from the English Purbeck. In his revision of the Wealden and Purbeck fishes, Woodward (1918) transferred these two species to a new genus, *Enchelyolepis*.

REMARKS. Woodward's description of the two specimens known of this genus is adequate. However, the specimens are important in that they display the endoskeleton of the caudal fin; this remains unknown in other macrosemiids. A redescription of this important region is given below.

Enchelyolepis pectoralis (Sauvage 1883)

Fig. 21

1883 *Macrosemius pectoralis* Sauvage : 477; pl. 12, fig. 17.
1895 *Macrosemius pectoralis* Sauvage; Woodward : 179.
1918 *Enchelyolepis pectoralis* (Sauvage) Woodward : 81; pl. 17, fig. 7.
1966 *Enchelyolepis pectoralis* (Sauvage); Schultze : 276; text-fig. 34.

DIAGNOSIS. *Enchelyolepis* with very broad, laterally-compressed neural arches and spines.

HOLOTYPE (and only specimen). BM(NH): P7359.

HORIZON AND LOCALITY. Upper Portlandian of Savonnières-en-Perthois, Meuse, France.

DESCRIPTION. See Woodward 1918 : 81; pl. 17, fig. 7. Much of the internal skeleton of the caudal fin in this specimen is preserved in impression (Fig. 21). Four rays emerge from the axial lobe of the fin, and only five branched rays occur below this, preceded by three short, unsegmented rays. Since all other adult macrosemiids possess eight segmented lower rays, the three unsegmented lower rays have probably not reached their adult length. In young specimens of *Notagogus pentlandi* Agassiz too, only five or six of the lower rays are long and segmented; there are eight in the adult. The lower rays articulated upon six axial supports of which two have survived in the specimen (the rest have left impressions); they form stout cylindrical rods. Since the haemal arches in this region are not preserved, there is nothing to indicate which of these are hypurals.

The epaxial region of the fin is traversed by one short and four elongated elements; the last two of these articulated with the dorsal basal fulcra. Woodward (1918 : 81) identified them as neural arches, but in the specimen of *E. andrewsi* (P6303), in which these bones are entirely preserved, they are unpaired and are thus neural spines or epurals. In fact all these elements except the third are free from their neural arches and are thus epurals. The small ural neural arches, traces of which

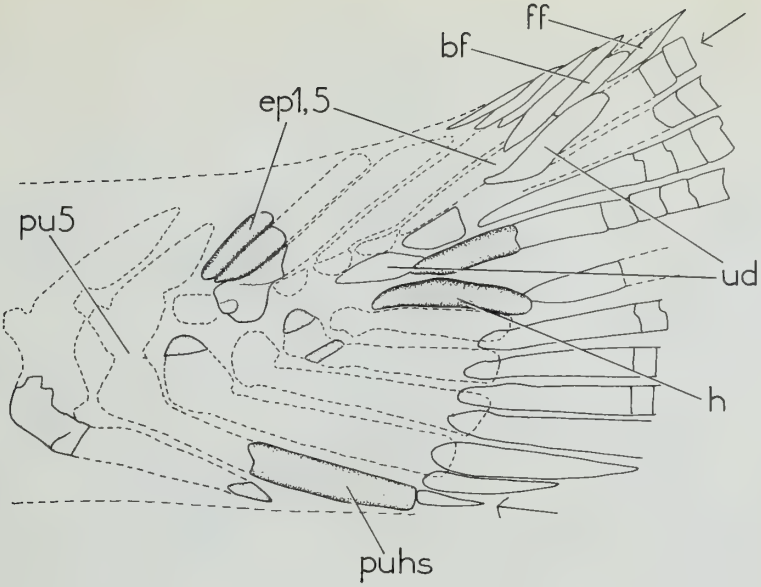

Fig. 21 *Enchelyolepis pectoralis* (Sauvage). Caudal fin, as preserved in P7359; the dashed lines denote impressions in the matrix. × 12.

remain, were not elongated. Three urodermals, remnants of the rhomboid squamation of the axial lobe, are also preserved.

The trunk scales are, remarkably, cycloid. Schultze (1966 : 276, text-fig. 34) has drawn three of them and noted their similarity with those of *Amia* in the radial markings on the anterior overlapped region.

Enchelyolepis andrewsi (Woodward 1895a)

1895a *Macrosemius andrewsi* Woodward : 148; pl. 7, fig. 3.
1895 *Macrosemius andrewsi* Woodward; Woodward : 180.
1918 *Enchelyolepis andrewsi* (Woodward) Woodward : 80; pl. 17, fig. 6.

DIAGNOSIS. *Enchelyolepis* with more slender haemal arches and neural spines than those of *E. pectoralis.*

HOLOTYPE (and only specimen). BM(NH): P6303.

HORIZON AND LOCALITY. Middle Purbeck of Teffont, Wiltshire, England.

DESCRIPTION. See Woodward 1918 : 80; pl. 17, fig. 6.

Genus ***PROPTERUS*** Agassiz 1834

DIAGNOSIS. Small to medium-sized macrosemiid fishes; trunk somewhat deepened and irregularly fusiform with the dorsal profile slightly bent at the level of the first dorsal fin-ray; supratemporals reduced; supratemporal commissure largely surrounded by parietals, whose surfaces are raised into strong ridges bearing ganoine; frontoparietal suture serrate; cranial division of main lateral line exposed by large fenestrae in dermopterotic; vomers bearing a single row of tall, pointed teeth; ventral parts of first three infraorbitals overlapping the maxilla; gape very small, the jaw articulation lying anterior to the orbit; premaxillary teeth tall and pointed; dentigerous expansion of maxilla symmetrical, the upper and lower edges straight, diverging, the hind border convex, teeth greatly reduced in size and number; mandible with closely-set teeth on dentary, medial wall of sensory canal trough in articular perforated by small pores; lateral border of palate rising steeply from jaw articulation; anterodorsal edge of metapterygoid forming an obtuse angle; leading edge of preopercular following a smooth curve; opercular ornamented with small tubercles of ganoine, uppermost branchiostegal ray devoid of ganoine; single vertical row of denticles on cleithrum; vertebral centra, in form of dorsal crescents, restricted to predorsal region of notochord; pectoral fin with about 16 rays and six proximal radials, hemitrichia of leading ray incompletely fused together, fringing fulcra absent; pelvic fin comprising six rays preceded by basal and fringing fulcra; base of anal fin compact, leading ray extending below caudal fin, preceded by basal and fringing fulcra; dorsal fin divided with at least some rays of the anterior part taller than those of the posterior part; caudal fin deeply forked, with between six and eight rays on the axial lobe, fringing fulcra on both borders; squamation entire, regular, lateral trunk scales deeper than broad, posterior edge slightly convex, anterior ventral scales cycloid.

TYPE SPECIES. *Propterus microstomus* Agassiz 1834.

INTRODUCTION. The genus *Propterus* was erected by Agassiz (1834) to include a single species from the Lower Kimmeridgian of Bavaria, *P. microstomus*. Wagner (1851, 1863) added *P. gracilis*, *P. speciosus* and *P. elongatus* from the same locality.

Woodward (1895) transferred Costa's (1850) *Rhynchoncodes scacchi*, from the Lower Cretaceous of Castellamare near Naples, to *Propterus*. Also, he considered *P. gracilis* and *Notagogus zieteni* (Agassiz 1835) to be synonymous with *P. microstomus*. Sauvage (1903) described *P. vidali* from the Neocomian of Lerida, Spain, and Eastman (1914a) recorded a new species from Bavaria, *P. conidens*. More recently Vianna (1949) recorded a specimen of *P. microstomus* from the Lusitanian of Portugal.

REMARKS. Wagner (1851) gave a short description of *P. speciosus*. Since his specimen appears to differ from Agassiz's *P. microstomus* only in its larger size, it is here taken to belong to Agassiz's species.

Woodward (1895) referred several specimens in the British Museum to *P. speciosus*. However, the anterior dorsal fin of these specimens is tall throughout its length; in contrast the very long anterior dorsal fin-rays of *P. speciosus* decline rapidly in height to produce a falcate fin. Examination of the type specimen of *P. elongatus* (Wagner 1863) reveals that in this species too the anterior dorsal fin shows no great variation in height along its length, although Wagner did not mention this in his description and gave no drawing of the specimen. Woodward's specimens agree with *P. elongatus* in their proportions as well as in the shape of the dorsal fin, and are thus referred to this species here.

Eastman (1914a) followed Woodward in assigning the Carnegie Museum specimens to *P. speciosus*; these too belong to *P. elongatus*. Also, *P. conidens* Eastman is indistinguishable from *P. microstomus*.

P. elongatus will be described first since this is the best known species.

Propterus elongatus Wagner 1863

Pls 3–4; Figs 22–30

1863 *Propterus elongatus* Wagner : 645.
1881 *Notagogus macropterus* Vetter : 46.
1881 *Histionotus parvus* Vetter : 48; pl. 2, fig. 5.
1895 *Propterus speciosus* Wagner; Woodward : 184, pl. 3, fig. 5.
1914a *Propterus speciosus* Wagner; Eastman : 407, pl. 13, fig. 1.

DIAGNOSIS. *Propterus* reaching standard length of 130 mm; mean proportions as percentages of standard length: head length 34%, trunk depth 36%, predorsal length 42%, prepelvic length 58%, preanal length 79%; fin-ray counts: D(ant.) 14–16, D(post.) 14–16, P 17, V 6, A 5, C 14–15; about 37 lateral line scales; scales thin with large serrations; two lobes of dorsal fin very close together; outline of anterior dorsal convex; fulcra absent from posterior dorsal; caudal fin-rays bifurcating a maximum of twice.

HOLOTYPE. Bayerische Staatssammlung für Paläontologie und historische Geologie, München, AS.1.767.

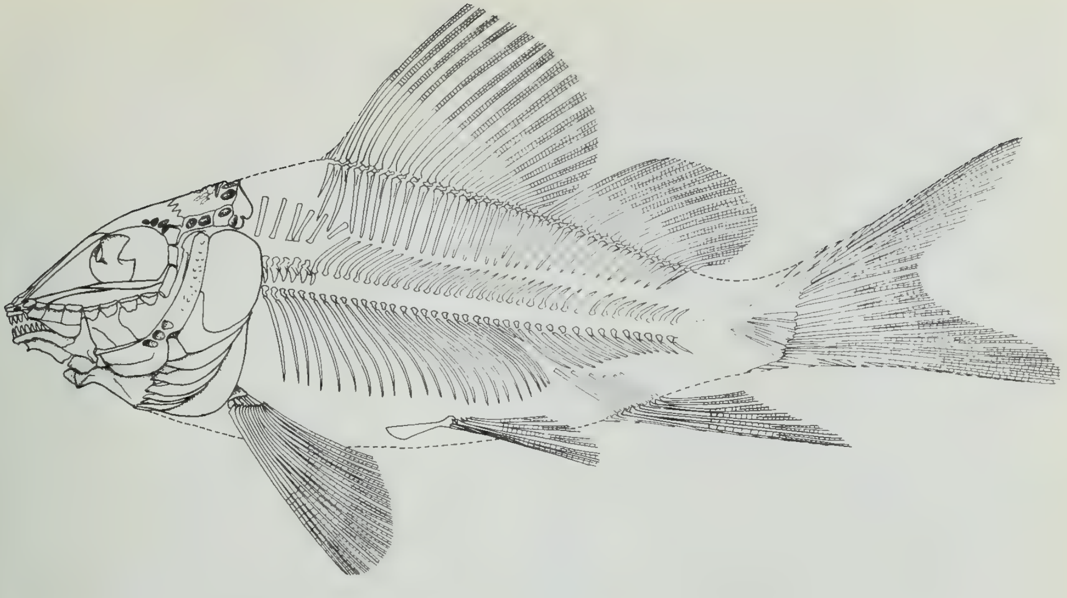

Fig. 22 *Propterus elongatus* Wagner. Restoration of skeleton with scales omitted. × $\frac{4}{5}$ approx.

HORIZON AND LOCALITIES: Lower Kimmeridgian of the Eichstätt region, Bavaria, Germany.

MATERIAL. BM(NH): 37935a & b, 37099, 37088, P5547; RSM: 1893.120.5; Mü: 1964.23.145, AS.1.767; CM: 4718, 4824; Ei: four specimens.

REMARKS. Vetter's (1881) incomplete specimen of *H. parvus* most probably belongs to this species, as does his *N. macropterus*. As explained above, Woodward's specimens of this species were incorrectly ascribed to *P. speciosus*.

DESCRIPTION. (i) General features. *P. elongatus* displays the characteristic form of the genus, in which the depth of the trunk decreases posteriorly from the level of the first dorsal fin-ray to form a narrow caudal peduncle (Fig. 22). Most specimens are about 100 mm in length.

(ii) Skull roof and braincase. The skull roof is exposed in dorsal view in the acid-prepared specimen 1964.23.145 (Fig. 23). It resembles that of *Macrosemius* in its general proportions, although the preorbital region of the frontals is shorter in comparison with the postorbital region.

The parietal has similar relationships to the surrounding bones as in the type genus; in contrast, however, the frontoparietal suture is serrated. As usual, the supratemporal commissure passed through the parietal close to the posterior border; the canal was exposed dorsally by a single fenestration, and also along a short distance across the midline as it passed from one parietal to the other. Anterior to the commissure the surface of the parietal forms stout, radiating ridges bearing tubercles of ganoine. These ridges decrease in height and disappear before the suture with the frontal is reached. The anterior and middle pit-lines form short, deep grooves, lying at about 45 degrees to each other, across the ridges.

The supratemporal is not preserved; it must have been very similar in form and position to that of *Macrosemius*. The right dermopterotic is preserved in a crushed state. It resembles that of the type genus; the wide sensory canal was exposed by two or three large fenestrae.

The frontal forms a straight median suture with its fellow; its surface is devoid of ganoine and bears no ridges. The supraorbital sensory canal entered the bone through a lateral opening immediately behind the orbit. As the canal passed medially it was exposed by three fenestrae of regularly decreasing size aligned close to the posterior border of the orbital embayment of the frontal. Between the embayments the canal converged gradually with the midline; it was exposed in this region by one small and two elongated openings facing medially and giving onto the sunken surface of the frontal alongside the median suture. A bundle of extremely fine diverging tubes extends from the canal tube midway above the orbit to the surface of the bone in the anterior part of the orbital region. A number of much shorter tubes extends from the posterior part of the canal, following a curved path to the surface. Anterior to the orbit, as usual, the frontal forms an open trough which housed the supraorbital sensory canal.

The nasal is not preserved; it probably formed a scroll around the sensory canal as usual.

The rostral is visible in ventral view in 1964.23.145. It enclosed only a short length of the rostral commissure on either side of the midline. The bone forms two broad wings which lay above the anterior ends of the antorbitals.

The vomerine teeth are exposed from below in 1964.23.145 (Fig. 26). These are tall and conical,

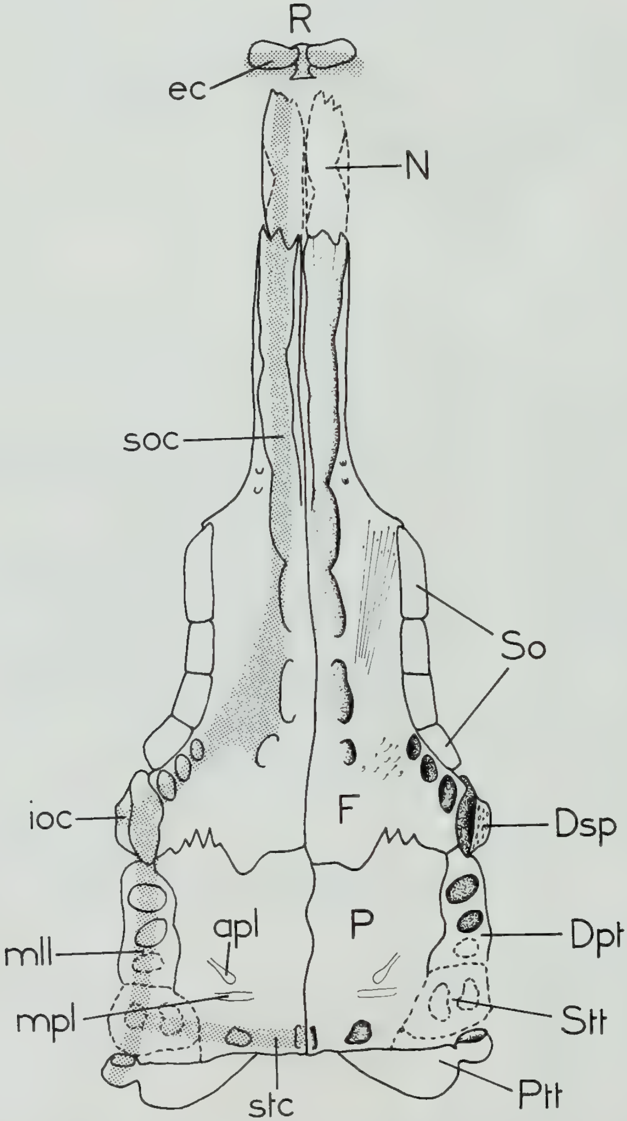

Fig. 23 *Propterus elongatus* Wagner. Skull roof, as preserved in 1964.23.145. Dashed lines indicate restored parts. × 6.

and form a single transverse row posterior to and parallel with the premaxillary tooth-row, as in the type genus. Each vomer bears about six teeth.

The parasphenoid is stout and curves downwards slightly to the snout region. Its lateral borders form a narrow suborbital shelf. A stout basipterygoid process, similar to that of *Macrosemius*, is visible in 37099.

The orbitosphenoid (Fig. 24) is a large bone reaching from the parasphenoid to the skull roof and presenting in lateral profile the form of an incomplete disc, with a deep, concave emargination in the posterodorsal quadrant. A stout flange extends laterally from the dorsolateral surface. The posterior surface of this flange is smooth, presumably for the reception of the eyeball.

(iii) Circumorbital series. Supraorbitals are present in only one of the specimens (37935b); they have been lost from, or were absent in, the others. They number four; the foremost is the longest and tapers anteriorly. The central two are rectangular and the posterior one triangular.

There are ten bones, as in all macrosemiids, in the infraorbital series. The antorbital consists of a simple tube, tapering as it turns medially towards the rostral (Figs 24, 26); the lateral wall is pierced by several large fenestrae occupying the entire width of the tube.

The first seven scroll-like infraorbitals, lying below the level of the parasphenoid, are preserved in 37935 and 1893.120.5. As in *Macrosemius*, the anterior three extend ventrally to cover the lateral surface of the maxilla; their edges in contact are straight. The following four infraorbitals extend to the level of the basipterygoid process; their arrangement and form are very similar to those of the type genus. The eighth and ninth members of the series form the usual perforated tubes around the upper part of the infraorbital canal; as in *Macrosemius*, the lower is about twice the length of the upper.

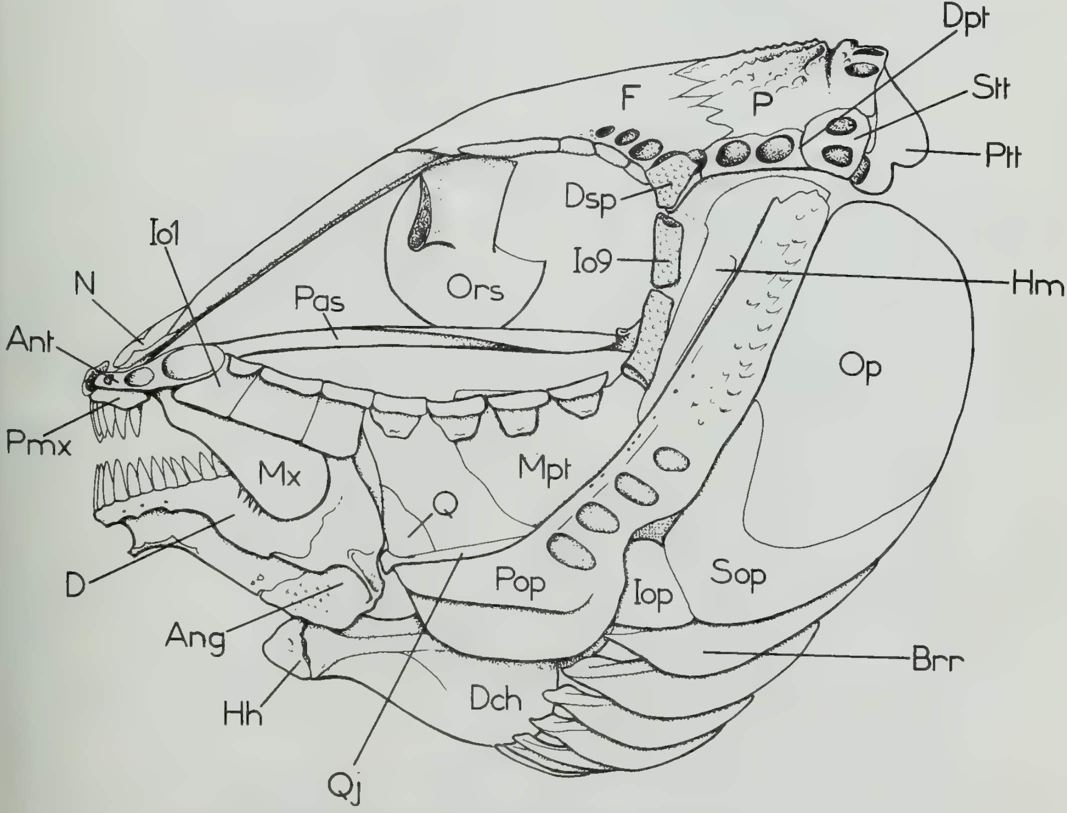

Fig. 24 *Propterus elongatus* Wagner. Restoration of skull. × 5 approx.

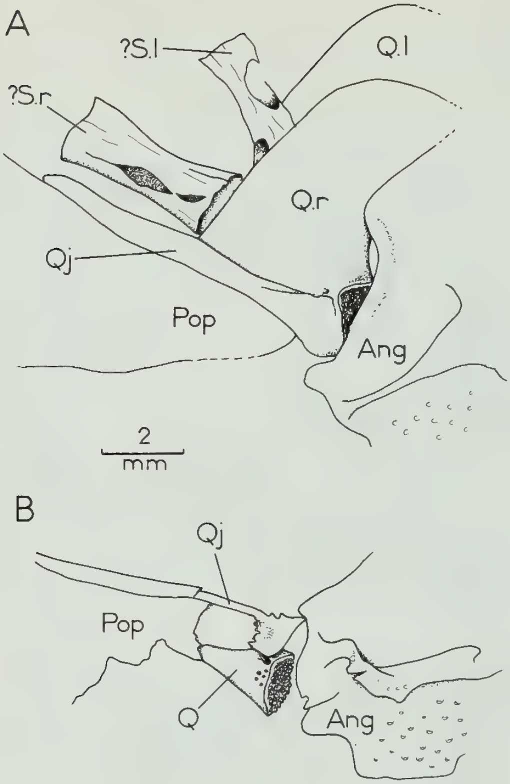

Fig. 25 *Propterus elongatus* Wagner. Lateral views of right jaw articulation, as preserved in A, 1893.120.5 and B, 1964.23.145.

The dermosphenotic is again typical of the family; it forms a short, perforate tube, with a flared dorsal end, which lies against the lateral surface of the sphenotic. Its anterior wall is not prolonged dorsally (1964.23.145).

(iv) Hyopalatine bones. None of the specimens displays the palate in its entirety. The oral border of the palate rises much more steeply from the jaw articulation than it does in *Macrosemius*. A few tall ectopterygoid teeth are visible in 1964.23.145 (Fig. 26). The metapterygoid is much as it is in the type genus; this bone contacts the quadrate only in the larger specimens. The hyomandibular is not fully exposed in the specimens, although in one of them (37099) the lateral flange may be seen.

The quadrate is exposed in 1893.120.5. Its long dorsoposterior edge is slightly convex (Fig. 25A). The quadratojugal is slender, extending for about twice the length of the quadrate against which it lies. The shaft of the bone is slightly expanded laterally midway along its length; it rests as usual upon the upper surface of the ventral arm of the preopercular. Distally the shaft expands and abuts against the lateral surface of the quadrate condyle; it is not clear from this specimen whether fusion occurs between the two bones in this region as it does in *Macrosemius*. In another (1964.23.145), however, the preopercular and quadratojugal have together been twisted through about 90 degrees, away from the quadrate. The expanded head of the quadratojugal has pulled away quite cleanly from the quadrate and the two bones evidently were not fused (Fig. 25B). This specimen also shows clearly two notches on the lateral surface of the quadratojugal head.

In specimen 1893.120.5 (Fig. 25A) there lies a short stout bone, about four times as long as broad, in the space between the metapterygoid and quadrate. The remains of a similar element are associated with the quadrate of the left side. The crushed, flattened state of these bones indicates their origin in cartilage. Although probably displaced dorsally from its position in life, this element is probably the symplectic, a bone which has not been found in any other macrosemiid specimen, perhaps due to faulty preservation. There can be little doubt, however, that if present it formed no articulation with the mandible as it does in *Amia* and the extinct halecomorph holosteans (Patterson 1973). In most other groups the symplectic extends along the medial surface of the quadrate, although in certain forms in which the jaw articulation is very forwardly placed, for example *Lepisosteus* and some teleosts such as *Chanos* (Gosline 1967 : 238, text-fig. 1), contact between symplectic and quadrate is almost or entirely lost. A tendency towards this condition appears to be exhibited by *Propterus.*

(v) Dermal upper jaw. The head of the premaxilla is broad and bears six tall, pointed teeth similar to those on the vomer. The point of each tooth is formed by a cone of enamel. The nasal process of the premaxilla is not exposed in the specimens.

The upper and lower borders of the maxilla diverge posteriorly from the medial process; the hind edge is convex. A row of very small needle-like teeth occupies the posterior half of the oral border.

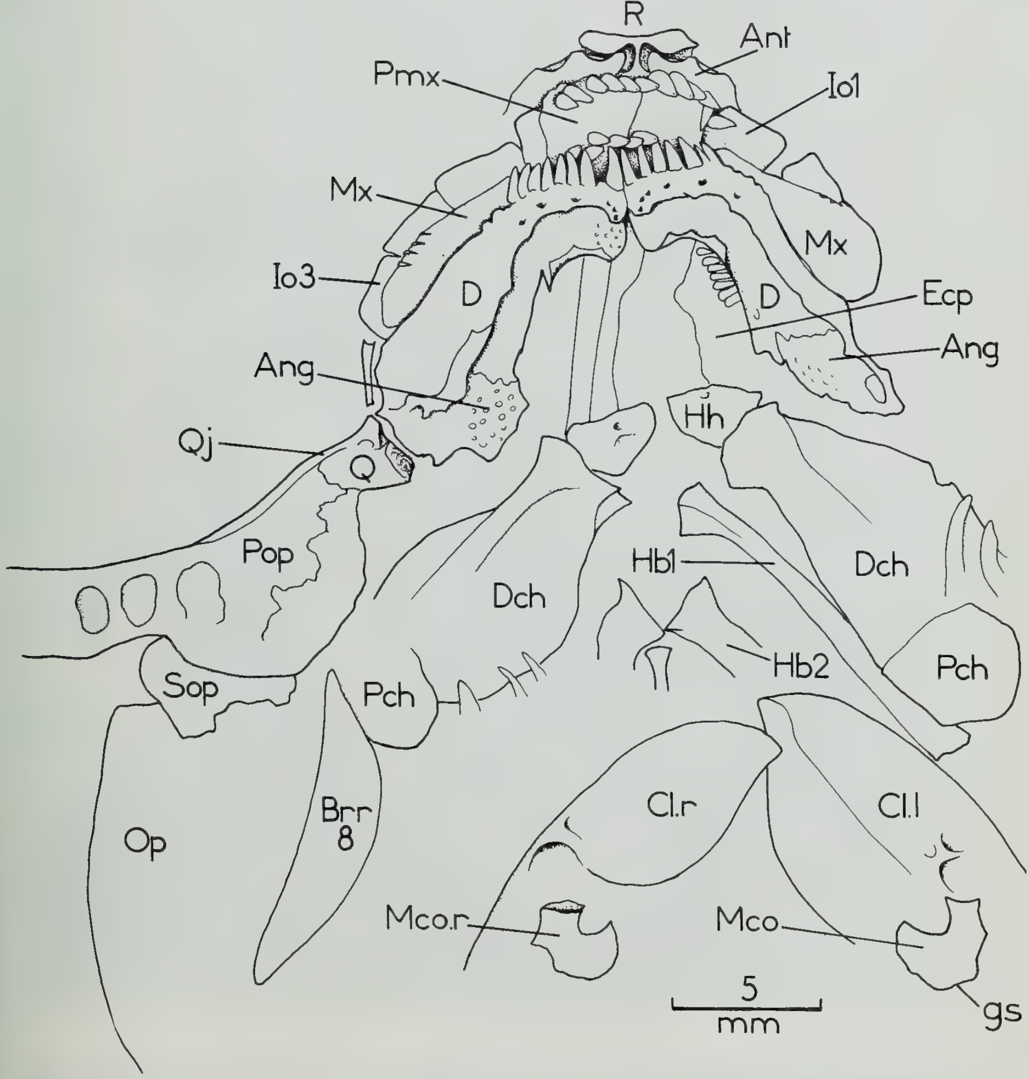

Fig. 26 *Propterus elongatus* Wagner. Dorsoventrally-crushed skull in ventral view, as preserved in 1964.23.145.

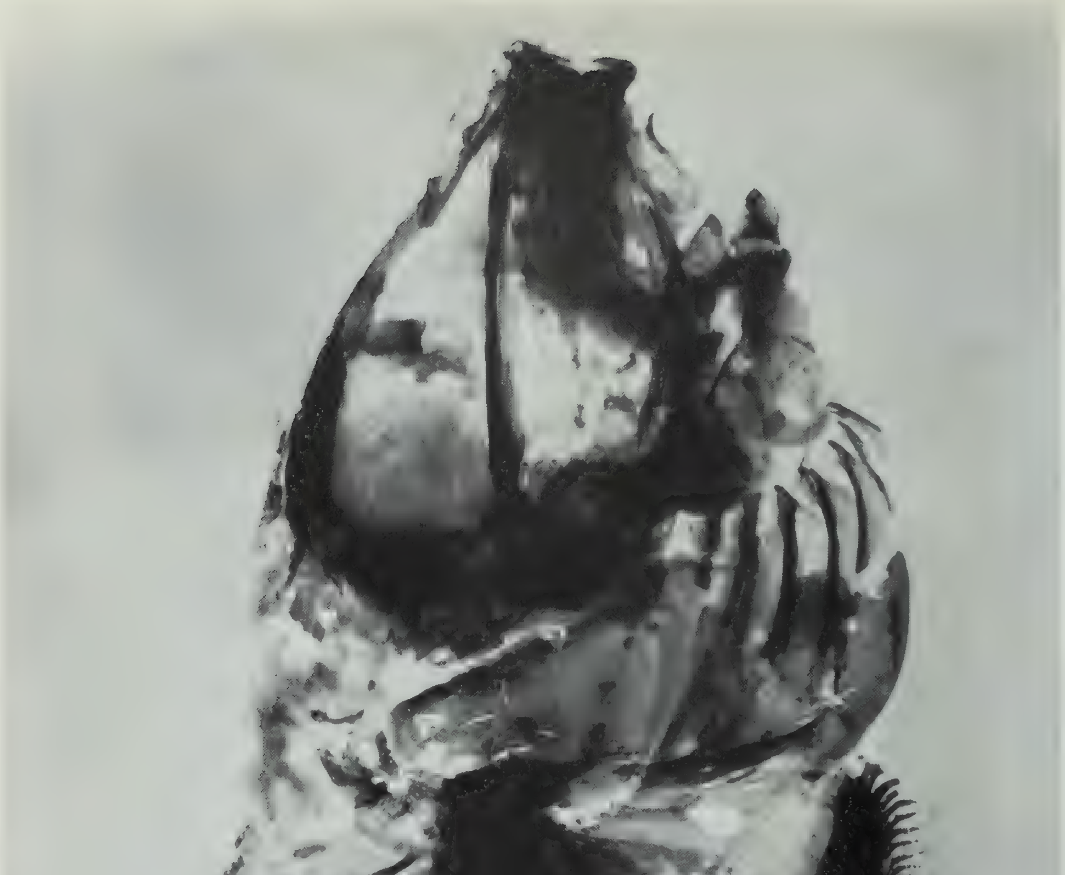

Plate 3 *Propterus elongatus* Wagner. Positive print of a radiograph of the skull and anterior part of the trunk, transfer preparation of 1893.120.5. ×3.

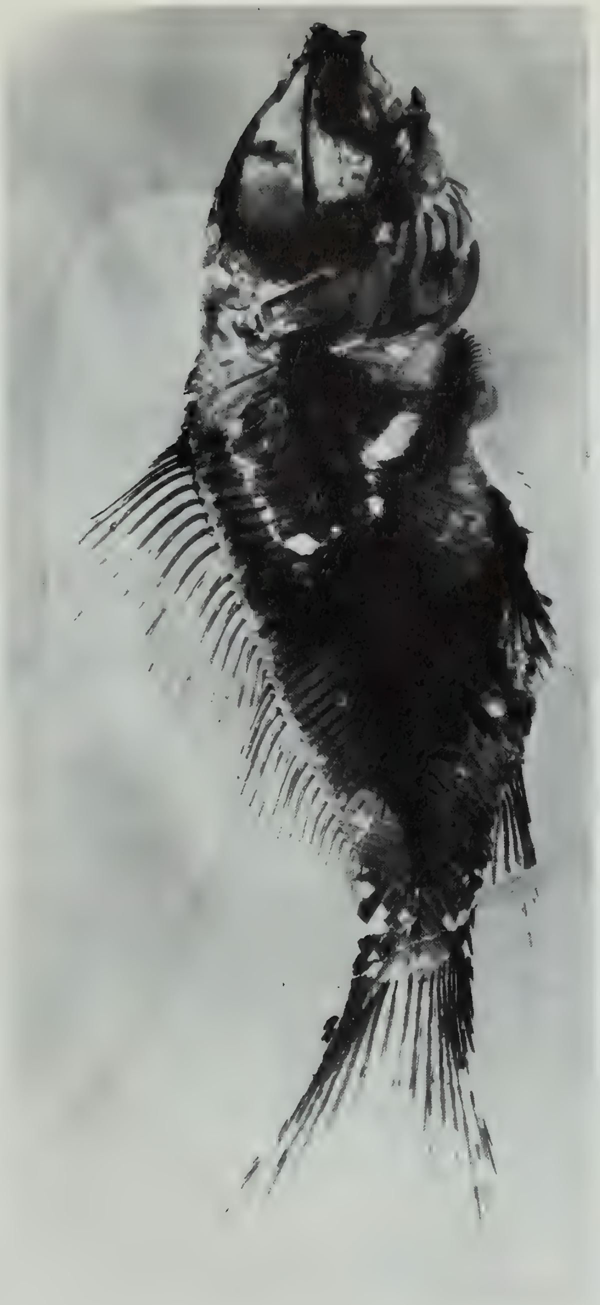

Plate 4 *Propterus elongatus* Wagner. Positive print of a radiograph, transfer preparation of 1893.120.5. × 1·125.

(vi) Lower jaw. Only the dentary and angular bones can be described from the specimens. The dentary bears about 11 teeth; these are tall and closely set, resembling those of the premaxilla. A series of six foramina pierce the dentary below the tooth-row. As in other macrosemiids the mandibular sensory canal lay in a very wide, open trough in the dentary. The canal continued along a trough formed by the angular; in contrast to the condition in *Macrosemius* a complete, slender arch of bone spanned the canal below the quadrate articulation. The medial wall of the trough is pierced by many small holes, and forms an interdigitating suture with the dentary. Above the canal the angular forms a long slender prolongation which passes along the upper edge of the canal as in the type genus.

(vii) Preopercular, hyoid arch and opercular series. The fore edge of the preopercular follows a regular curve from the skull roof to the jaw articulation. The lower part of the dorsal arm is pierced by large fenestrae (two in 37935b, four in 1893.120.5) which exposed the sensory canal. In the upper part of the dorsal arm the canal communicated with the exterior through many dorsally-directed pores (Fig. 24). As in other members of the family, the lower surface of the canal was exposed along the entire length of the ventral arm of the preopercular.

The opercular is narrow, about twice as deep as wide. The outer surface of the bone is slightly wrinkled and bears small, pointed, isolated tubercles of ganoine (1964.23.145). The subopercular forms the usual vertical process along the leading edge of the opercular; its surface is smooth and devoid of ganoine. The interopercular is, as in other macrosemiids, small and remote from the mandible. There are seven or eight branchiostegal rays; the upper rays are acinaciform. Their blades are deeper than those of *Macrosemius*. The condition of the uppermost ray cannot be determined from the specimens.

The ceratohyals are exposed in 1964.23.145. Both proximal and distal ossifications are closely similar to those of the type genus. The single hypohyal is also visible in this specimen. It consists mainly of cancellous endochondral bone bounded on its ventromedial surface by perichondral bone in the form of a laterally-buckled disc (Fig. 26); the centre of the disc is pitted, presumably at the point of insertion of the tendon of the sternohyoideus muscle.

(viii) Branchial arches. The elongated slender first hypobranchial is exposed in 1964.23.145. The anterior ends of the stouter second hypobranchials are also visible.

(ix) Vertebral column. There are about 40 vertebral segments between the skull and the base of the axial lobe. The column is not exposed in any of the specimens, but information about its structure can be obtained from a radiograph of the acid-prepared specimen 1893.120.5 (Pl. 4). Six median supraneurals occur behind the skull; the anterior four lie in front of the dorsal fin, and the remaining two interdigitate between the second and third and between the third and fourth proximal dorsal radials respectively. The first six vertebral segments appear to form dorsal crescentic hemicentra only; the remainder of the axis forms no centra. The same radiograph reveals that the neural spines are paired throughout the first 29 segments at least. There are about 20 pairs of abdominal ribs.

(x) Pectoral girdle and fin. The post-temporal forms a triangular lamina which articulated in a groove along the posterior edge of the parietal. The lateral part of the bone is not preserved; it probably formed an inflated tube around the cephalic division of the main lateral line as in other macrosemiids.

The cleithrum is exposed in lateral view in 37935b (Fig. 27). The anteromedial edge of the ventral arm forms two shallow embayments; the posteroventral edge is gently convex. A single row of denticles, each bearing a single cusp, is aligned vertically along the lateral face of the dorsal arm. The dorsolateral surface of the ventral arm forms a rounded zone for the lower part of the opercular membrane, as is usual. The lower surface of this rounded region is exposed in 1964.23.145 (Fig. 26); it is defined medially by a ridge which presumably also marked the limit of the insertion of the ventral trunk musculature. Immediately posterior to the ridge occurs a deep recess for the reception of the endoskeletal pectoral girdle.

The ossified part of the scapulocoracoid forms a simple stout arch of bone (Fig. 26). One foot of the arch forms a broad surface which fitted into the recess on the cleithrum; the other foot presumably continued as an anterior cartilaginous process which in life made contact with the ventral surface of the cleithrum, as in *Lepisosteus* (Jessen 1972: text-fig. 4). The glenoid surface for the articulation of the proximal radials of the fin occurs on the outer part of the arch.

The endoskeleton of the fin is not clearly preserved; there appear to be five proximal radials increasing in length posteriorly. There are about 15 pectoral fin-rays. The leading ray, devoid of basal and fringing fulcra, consists of two fused hemitrichia terminating below the segmented part of the succeeding ray (Fig. 28B). The leading ray is not as reduced as that of *Macrosemius rostratus*, however, and shows signs of incomplete fusion between the two hemitrichia; it bears dorsally- and ventrally-directed processes at its base, as do the remaining rays, which are segmented and branch distally.

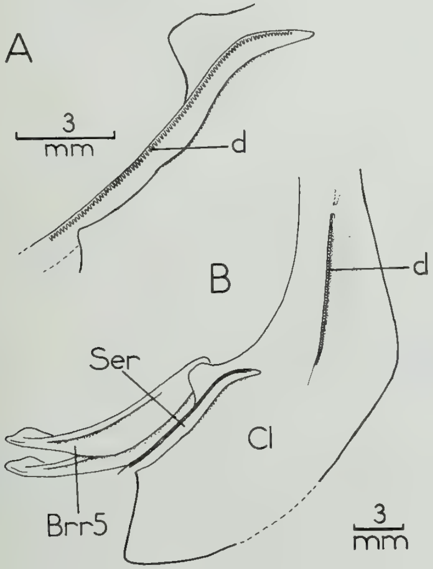

Fig. 27 *Propterus elongatus* Wagner. Part of pectoral girdle, as preserved in 37935b. A, left serrated appendage. B, part of left cleithrum, serrated appendage and two branchiostegals.

A slender serrated appendage is preserved in 37935 lying along the upper margin of the ventral arm of the cleithrum. The distal end of the bone tapers and turns posteriorly; it appears to have projected into the opercular cavity. A single row of denticles, similar to those of the cleithrum, extends along the lateral surface close to the leading edge (Fig. 27). The homologies of the serrated appendage are discussed below (pp. 216–7).

(xi) Pelvic fin. This consists of six rays. The leading ray is preceded by four stout basal fulcra and a thick saddle-shaped scale devoid of denticles (Fig. 28A). The first two basal fulcra are unpaired and short, with broad bases. The third is twice the length of the second and is also unpaired, although cleft almost to the tip. The last basal fulcrum is paired and succeeded by fringing fulcra. All the rays are jointed and bifurcate twice. The hemitrichia form anterolaterally-directed flanges at their bases which overlap the preceding ray, thus forming a very compact fin base.

(xii) Dorsal and anal fins. The dorsal fin is divided; it extends from the dorsal angulation of the body to the caudal peduncle. In this species both the anterior and posterior parts of the fin are tall, with a convex outline. The two parts are very close together; there are between 14 and 16 fin-rays in each. The anterior dorsal is preceded by about seven slender basal fulcra. The leading ray is unpaired and unsegmented and extends slightly beyond the basal segment of the second ray. The first three radials consist of the proximal ossification and presumably the distal cartilaginous part alone; the middle segment is absent. The remainder of the fin-rays articulated with tripartite radials as usual. The posterior lobe of the dorsal fin, arising above the 20th vertebral segment, is completely devoid of fulcra and follows closely behind the anterior dorsal. The discontinuity in the fin is reflected in the inclination of the proximal radials; the proximal radial of the last anterior fin-ray is shorter than the others, and those of the posterior fin are inclined slightly backwards.

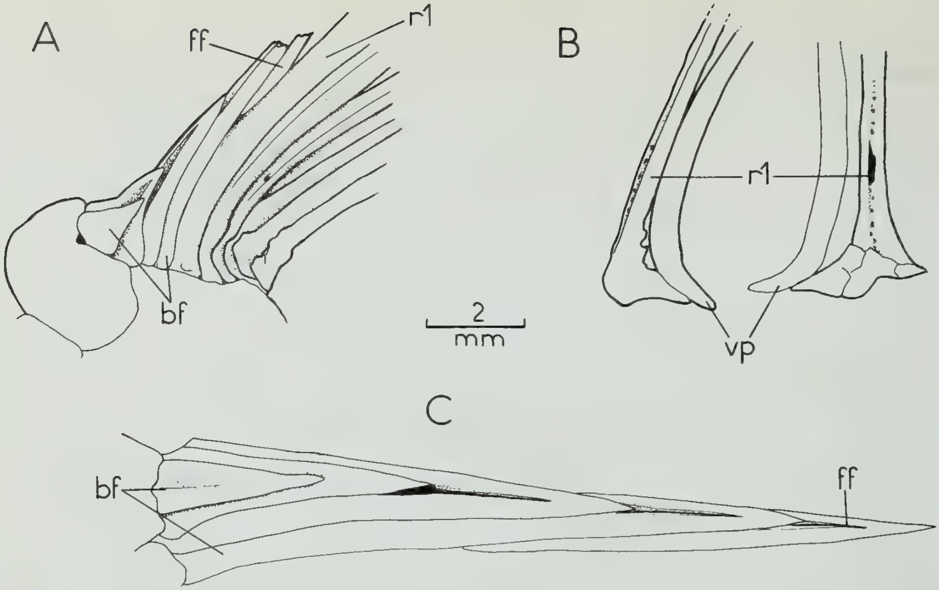

Fig. 28 *Propterus elongatus* Wagner. Bases of leading edges of various fins, as preserved in 1964.23.145. A, left pelvic fin. B, left and right pectoral fins. C, anal fin.

The anal fin was supported by six rays; it arises below the level of the 28th vertebral segment. Four unpaired basal fulcra extend along the proximal half of the leading edge of the fin. The third and fourth basal fulcra are cleft to within a very short distance of the pointed tip (Fig. 28C). The first fringing fulcrum is unpaired but again deeply cleft. The remainder of the fringing fulcra extending along most of the length of the leading ray are paired. The base of the anal fin is short and compact, in contrast to the condition in *Macrosemius*, and the first ray extends beneath the caudal fin. The remaining rays become progressively shorter, to form the slightly convex profile of the hind border of the fin.

(xiii) The caudal fin is deeply forked, with seven rays emanating from the axial lobe and eight, as usual, arising below this (Fig. 29B). The upper basal fulcra are deeply divided and extended basally, forming two tapering prongs which straddled and articulated with the epurals (Fig. 29A). The lateral borders of these fulcra taper posteriorly from the level of the cleft and then run parallel for a short distance before converging to a sharp point. The series continues along the uppermost fin-ray with about 13 fringing fulcra, of which the first eight (in 37099) are unpaired.

The uppermost fin-ray forms a continuation of the longest axial lobe scale-row and is not inserted below the squamation, as in the type genus. The following five rays form thin, closely-grouped rods proximally which penetrate beneath the axial lobe squamation and clasp the upper hypurals. The basal part of the lowermost axial lobe ray clasps the tip of its hypural and is separated from the upper rays, although its distance from the succeeding rays is greater. The ventral border of the caudal fin bears basal and fringing fulcra. The axial lobe squamation is described below.

(xiv) The scale-rows correspond to the segmentation; there are about 37 scales along the main lateral line and about 15 in the deepest transverse row. Most of the abdominal scales are deeper than wide, with the posterior edge denticulated and slightly convex; all the scales are thin. The most extensive ganoine covering on the scales occurs in the posterior half of the body, as in *Macrosemius*; anteriorly the ganoine is restricted to the hind region and to the denticles. The postcleithral scales are nowhere clearly exposed.

The ventral surface of the body between the pelvic and anal fins is visible in 1964.23.145; the scales in this region are roughly square. Denticles are present only on the median scales where they are few and large. There is a very large preanal scale and two lateral anal scales (Fig. 29). In contrast to those of the type genus, all three bear stout denticles and ganoine ridges.

The axial lobe squamation is not well preserved in any of the specimens, although it can be reconstructed from 1893.120.5. The lobe is larger in comparison with the remainder of the caudal area (Fig. 30) than it is in *Macrosemius*. There are about seven rows with the usual orientation. The scales are thick and bear dorsally-inclined serrations along their posterodorsal edges. The lateral line ends below the axial lobe.

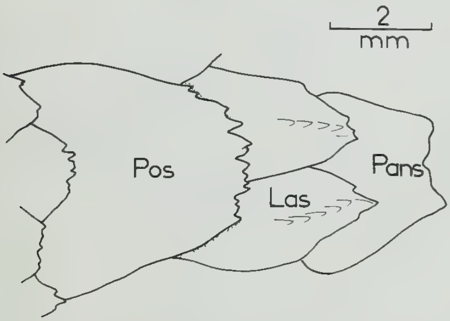

Fig. 29 *Propterus elongatus* Wagner. Circumanal scales, as preserved in 1964.23.145.

Propterus microstomus Agassiz 1834

Fig. 31

1834 *Propterus microstomus* Agassiz : 386.
1835 *Notagogus zieteni* Agassiz, **2** : pl. 49, fig. 1.
1839 *Propterus microstomus* Agassiz, **2** : pl. 50, figs 5, 6.
1844 *Notagogus zieteni* Agassiz, **2**, 1 : 10, 293.
1844 *Propterus microstomus* Agassiz, **2**, 1 : 296.
1851 *Propterus microstomus* Agassiz; Wagner : 66.
1851 *Notagogus zieteni* Agassiz; Wagner : 65.
1851 *Propterus gracilis* Wagner : 68.
1851 *Propterus speciosus* Wagner : 67; pl. 4, fig. 1.
1863 *Propterus microstomus* Agassiz; Wagner : 645.
1895 *Propterus microstomus* Agassiz; Woodward : 183.
1914a *Propterus microstomus* Agassiz; Eastman : 407; pl. 63, fig. 1.
1914a *Propterus conidens* Eastman : 407; pl. 62, fig. 2.
1949 *Propterus microstomus* Agassiz; Vianna : 13; pl. 1.
1966 *Propterus microstomus* Agassiz; Schultze : 275, text-figs 7, 31, 32; pl. 49, fig. 2.

DIAGNOSIS. *Propterus* reaching standard length of 150 mm, although most specimens are about half this size; mean proportions as percentage of standard length: head length 33%, trunk depth 38%, predorsal length 40%, prepelvic length 60%, preanal length 84%; fin-ray counts: D(ant.) 10–13, D(post.) 10–14, P 17, V 6, A 5, C 15; about 36 lateral line scales; scales thin; two lobes of dorsal fin separated by a gap; anterior dorsal fin outline concave; no fulcra on posterior dorsal fin; caudal fin-rays bifurcating a maximum of twice.

HOLOTYPE. Bayerische Staatssammlung für Paläontologie und historische Geologie, München, AS.7.268. From the Lower Kimmeridgian of Kelheim, Bavaria.

HORIZONS AND LOCALITIES. Lower Kimmeridgian of Eichstätt and Kelheim regions of Bavaria; Lusitanian of Cabo Mondego, Portugal.

MATERIAL. Mü: AS.7.268, AS.5.30, AS.1.634, AS.1.766, 1964.23.143, 1964.23.146; CM: 4468, 4825; Ei: five specimens.

REMARKS. As discussed above, the type specimen of Wagner's (1851) *P. speciosus* belongs to this species; so too does Eastman's (1914a) *P. conidens*. Details of the skull of *P. microstomus* remain

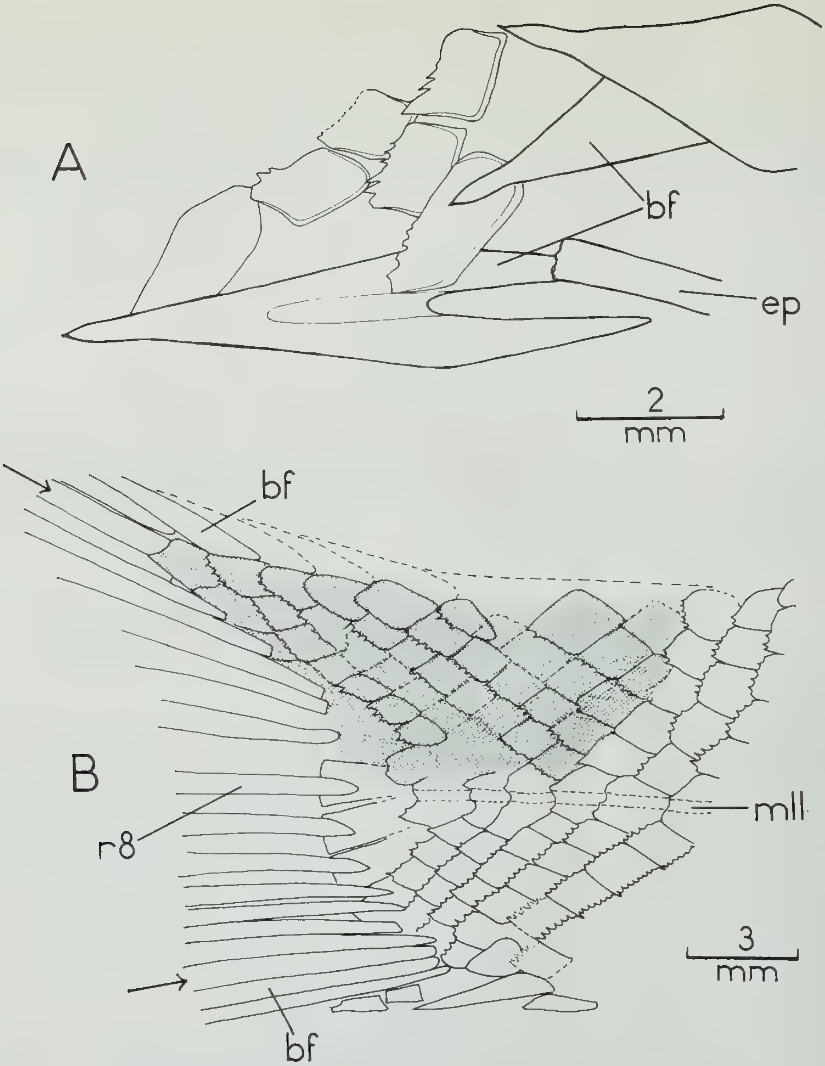

Fig. 30 *Propterus elongatus* Wagner. A, scattered dorsal basal fulcra of caudal fin, as preserved in 1964.23.145. B, caudal fin squamation restored from 1893.120.5, axial lobe shaded.

poorly known, since no specimens were available for preparation in acetic acid. However, this fish closely resembles *P. elongatus* in its form, proportions and squamation, and the available evidence indicates that their skulls were very similar as well.

Description. (i) General features. *P. microstomus* rarely exceeds 75 mm in standard length. It is the only member of the genus having an emarginated anterior dorsal fin (Fig. 31).

(ii) Dorsal fin. In contrast to the condition in *P. elongatus*, in which the two parts of the dorsal fin stand close together, these are separated by a distance equivalent to the width of four scales in *P. microstomus*. The leading ray exceeds the depth of the trunk in length; it is preceded by about seven basal fulcra and bears two elongated fringing fulcra. The 12 or so remaining rays of the anterior dorsal decrease rapidly in height, forming a deeply concave outline. The posterior dorsal fin, also comprising about 12 rays, is low and convex in outline.

(iii) Squamation. The number of rows and the pattern of the scales closely resemble those of *P. elongatus*. The ventral and circumanal scales have been drawn and described by Schultze

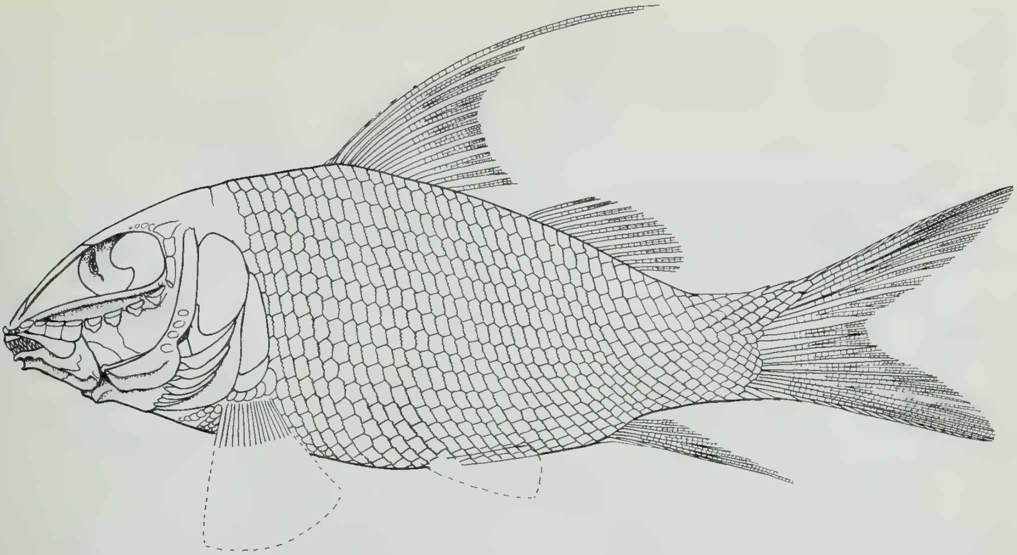

Fig. 31 *Propterus microstomus* Agassiz. Restoration of skeleton. × $\frac{3}{5}$ approx.

(1966 : 275, text-figs 7, 31; pl. 49, fig. 2). The ventral squamation is preserved in AS.1.634 and consists of about 20 rows at right angles to the main transverse rows; such an arrangement occurs in other groups, for example the chondrostean Haplolepidae (Westoll 1944 : text-figs 1, 13) and may be common to most actinopterygians with rhomboid scales. These scales tend toward a cycloid structure; they are rounded, lack ganoine and pegs-and-sockets, and bear both concentric and radial markings.

Propterus scacchi (Costa 1850)

1850 *Rhynchoncodes scacchi* Costa : 317; pl. 5, fig. 5.
1864 *Rhynchoncodes macrocephalus* Costa : 102; pl. 9, figs 10, 11.
1895 *Propterus scacchii* (Costa) Woodward : 185; pl. 3, fig. 6.
1912 *Propterus scacchi* (Costa); Bassani & d'Erasmo : 213; pl. 4, fig. 3.
1914 *Propterus scacchi* (Costa); d'Erasmo : 80; pl. 9, fig. 5.

DIAGNOSIS. *Propterus* reaching standard length of 60 mm; mean proportions as percentage of standard length: head length 37%, trunk depth 35%, predorsal length 48%, prepelvic length 65%, preanal length 88%; fin-ray counts: D(ant.) 10–11, D(post.) 10–11, A 6, C 14; outline of anterior dorsal fin convex; no fringing fulcra on posterior dorsal fin; caudal fin-rays branch a minimum of twice.

HOLOTYPE. Specimen in Universita di Napoli, Istituto di Paleontologia.

HORIZON AND LOCALITY. Lower Cretaceous (?Albian or Aptian) of Torre d'Orlando, near Castellamare, Naples, Italy.

MATERIAL. BM(NH): P3613.

REMARKS. Only Woodward's specimen was available for examination; little can be added to the early accounts by Italian workers.

Propterus vidali Sauvage 1903

1903 *Propterus vidali* Sauvage : 9; pl. 2, fig. 1.
1956 *Propterus vidali* Sauvage; Bataller : 114; pl. 14, fig. 1.

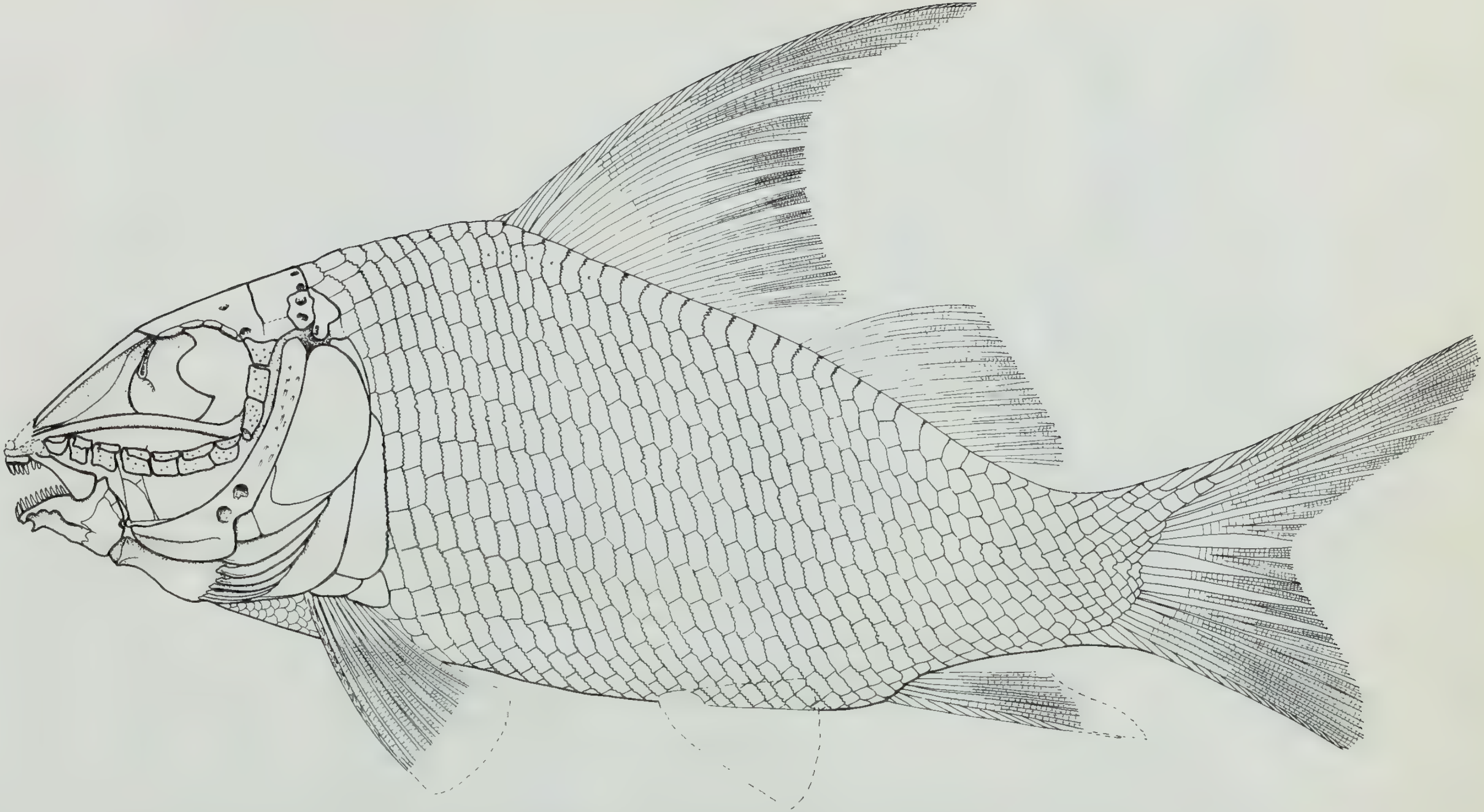

Fig. 32 *Histionotus oberndorferi* Wagner. Restoration of skeleton. Skull roof and infraorbitals restored from *H. angularis* Egerton. × $\frac{4}{5}$ approx.

DIAGNOSIS. *Propterus* reaching standard length of 130 mm; proportions as percentage of standard length: head length 27%, trunk depth 35%, predorsal length 43%, prepelvic length 50%, preanal length 75%; fin-ray counts: D(ant.) 10–11, D(post.) 10–11, C 14–15; about 35 lateral line scales; scales thick; outline of anterior dorsal fin slightly convex; fringing fulcra on posterior dorsal fin; caudal fin-rays bifurcate a maximum of six times.

HOLOTYPE. Specimen in Museo Municipal de Geologia, Barcelona.

HORIZON AND LOCALITY. Neocomian of Santa-Maria-de-Meya, Lerida, Spain (these beds have traditionally been treated as Kimmeridgian in age, like the classic localities of Germany and France, but recent micropalaeontological work (Brenner, Geldmacher & Schroeder 1974) shows them to be Neocomian, probably Valanginian).

MATERIAL. BM(NH): P10993, P10994.

REMARKS. This species is at present being studied by Mlle S. Wenz. The above provisional diagnosis, based upon the BM(NH) specimens, is given for comparison. The species is remarkable for the presence of fringing fulcra on the posterior dorsal fin, thick scales with very small pectinations and highly branched caudal fin-rays.

Genus *HISTIONOTUS* Egerton 1854

DIAGNOSIS. Medium to large, deep-bodied macrosemiid fishes; dorsal profile of trunk bent at first dorsal fin-ray; ganoine present on frontals and parietals, frontoparietal suture straight; supraorbitals large; gape very small, the jaw articulation lying anterior to the orbit; dentigerous expansion of maxilla pierced by small foramen, upper and lower borders concave, posterior edge convex, teeth absent or greatly reduced; dentary with closely-set styliform teeth; anterior edge of preopercular forming a smooth curve, sensory canal with many pores in dorsal arm; opercular, subopercular, interopercular and uppermost branchiostegal ray with radiating ridges of ganoine; leading ray of pectoral fin bearing long ridges of ganoine, probably fused fringing fulcra; base of anal fin compact, leading ray extending below caudal fin and bearing fringing fulcra; caudal fin deeply forked; dorsal fin divided, extending from dorsal angulation to the caudal peduncle, rays bifurcating profusely, leading ray bearing deeply overlapping fringing fulcra and greatly elongated, remaining rays of anterior dorsal decreasing rapidly in height to form a concave upper profile; posterior dorsal fin low, convex; vertebral centra forming thick cylinders; squamation forming pattern of deepened hexagons on trunk, scales adjoining dorsal fin each extended posteriorly along their dorsal edges and bearing pits of dorsal lateral line; postcleithral scales large, bearing ganoine ridges.

TYPE SPECIES. *Histionotus angularis* Egerton 1854.

INTRODUCTION. The genus *Histionotus* was erected by Egerton (1854) to contain one species, *H. angularis* from the Purbeck of southern England. Wagner (1863) described another species, *H. oberndorferi*, from the Lower Kimmeridgian of Bavaria, and Vetter (1881) added *H. parvus* from the same locality. Previously Thiollière (1873) had given a brief description of another species from the Lower Kimmeridgian of Cerin (Ain, France), *H. falsani*, of which Saint-Seine (1949) gave a fuller account. Finally, Eastman (1914a) added *H. reclinis* to the genus.

REMARKS. Vetter's (1881) imperfect specimen belongs to *Propterus elongatus* Wagner, and *H. reclinis* Eastman is an example of *Furo latimanus* Agassiz.

Histionotus angularis Egerton 1854

Figs 33–34

1854 *Histionotus angularis* Egerton : 434.
1855 *Histionotus angularis* Egerton; Egerton : 2; pl. 5.
1889 *Histionotus angularis* Egerton; Mansell-Pleydell : 241; pl. 7.
1895 *Histionotus angularis* Egerton; Woodward : 174.
1918 *Histionotus angularis* Egerton; Woodward : 77; pl. 17, figs 1–5.
1966 *Histionotus angularis* Egerton; Schultze : 306, text-fig. 48a.

Diagnosis. *Histionotus* reaching standard length of 150 mm; mean proportions as percentage of standard length: head length 30%, trunk depth 40%, predorsal length 37%, prepelvic length 53%, preanal length 77%; dentary teeth tall and styliform; the two lobes of the dorsal fin close together, with a total of *c.* 25 rays.

Holotype. British Museum (Natural History), P577.

Horizon and Localities. Purbeck Beds of Dorsetshire and Wiltshire, England.

Material. BM(NH): 46421, P577, P3614, P5935.

Remarks. Woodward (1918 : 77; pl. 17, figs 1–5) has given a detailed account of this species. The material is redescribed below, however, in the light of knowledge gained from other macrosemiid genera.

Description. (i) General features. *Histionotus angularis* is a deep-bodied, laterally-compressed fish; its average proportions are given in the diagnosis above.

(ii) Skull roof and braincase. The skull roof is displayed in P5935 and P577 (Fig. 33). The parietal is large and approximately rectangular, forming straight sutures with its fellow, the frontal, and the dermopterotic. The parietal contacts the supratemporal along an identation in its posterolateral corner. The supratemporal commissure crossed close to the posterior edge of the bone and was exposed dorsally by a small fenestration, as in *Propterus.* The canal emerged from its tube medially and crossed the midline unenclosed. Anterior to and parallel with the supratemporal commissure lies a short groove which housed the middle pit-line; no other pit-lines are visible. Thick ganoine rugae radiate from this region.

The supratemporal is, as usual, small, and does not reach the midline of the skull. Its irregular form is difficult to interpret in the specimens. It appears to have formed a wide thin-walled tube around the cephalic division of the main lateral line, together with a medial portion through

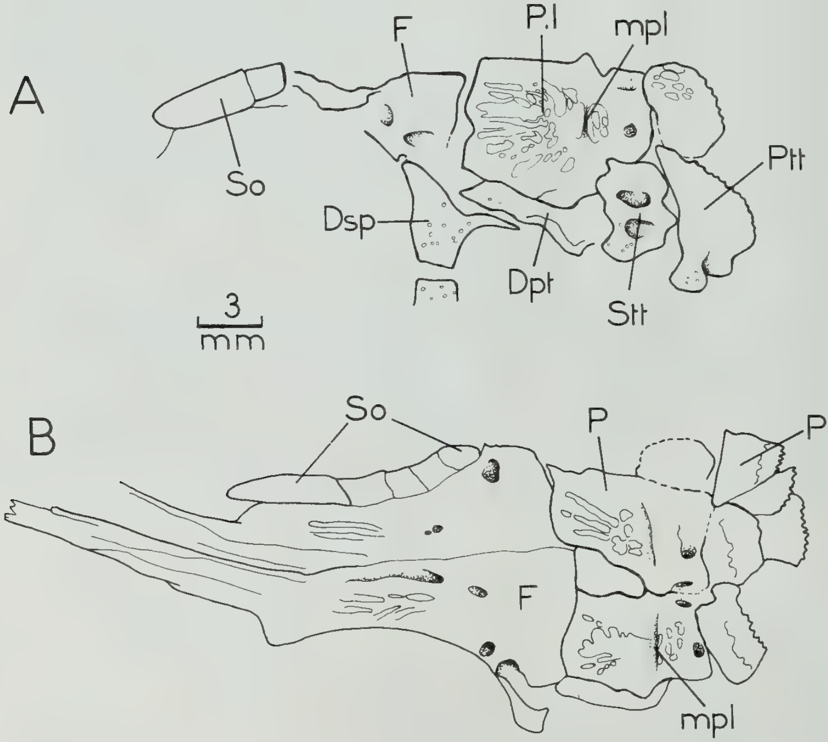

Fig. 33 *Histionotus angularis* Egerton. Skull roof, as preserved in A, P577 and B, P5935.

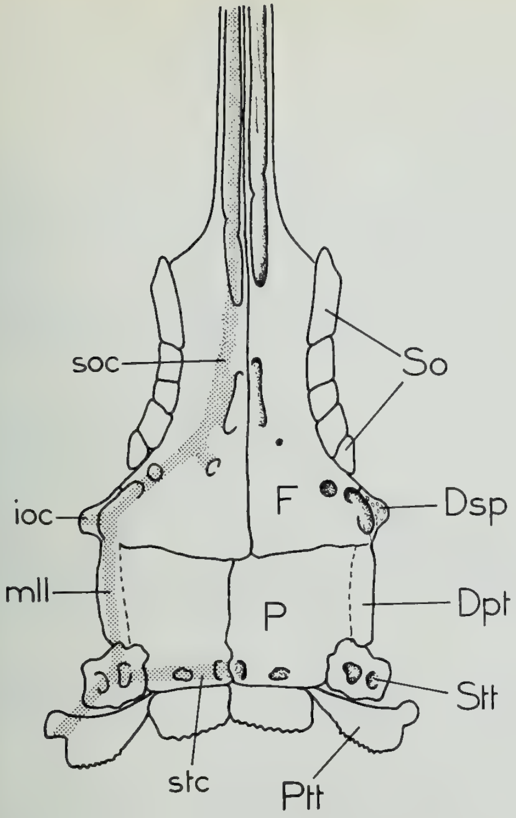

Fig. 34 *Histionotus angularis* Egerton. Restoration of skull roof. The probable medial limit of the dermopterotic is indicated by dashed lines; the nasals are omitted. ×4½ approx.

which passed the lateral part of the supratemporal commissure, where it was exposed by a large fenestration. The main lateral line continued anteriorly through the dermopterotic; the form of this bone is obscured by crushing in the specimens.

The short postorbital region of the frontal is wide, as usual. The supraorbital sensory canal entered the frontal laterally, behind the orbit, and passed medially; the canal in the supraorbital region is exposed by one or two elongated openings (Fig. 34), much as in *Propterus*. In the preorbital region the frontals form an open trough for the sensory canal as in they do all macrosemiids. They also form two lateral, vertical extensions on either side of the preorbital region of the skull; the frontals are similarly formed in *Notagogus*. Ganoine is restricted to two regions of the frontal. The smaller patch occurs close to the posterior border, while elongated rugae cover the surface between the orbital embayment and the sensory canal (Woodward 1918 : pl. 17, fig. 3).

The nasals are not preserved in the specimens. The orbitosphenoid is better known in *H. oberndorferi* described below; the remainder of the braincase remains unknown.

(iii) Circumorbital bones. There are five large supraorbitals, of which the foremost is the longest and tapers anteriorly. The remaining four are approximately rectangular; all bear a complex pattern of ridges on their surfaces.

The remains of the nine infraorbitals are discernible in P577; Woodward did not recognize them. The antorbital is crushed, but appears to have formed the usual tapering tube. The infraorbitals display the typical macrosemiid configuration; the first seven below the eye are curled over the infraorbital sensory canal, and the two behind the orbit form complete tubes.

The dermosphenotic, visible in P577, resembles that of *Macrosemius*. It forms a short, dorsally flared, vertical tube around the infraorbital sensory canal below its junction with the supraorbital canal. The anterior surface of the bone is prolonged into a stout process which abuts against the lateral margin of the frontal. Thus the dermosphenotic of *Histionotus*, while retaining the character of a member of the infraorbital series, was apparently firmly attached to the skull roof, as in *Macrosemius*.

(iv) Hyopalatine bones. A short portion of the ectopterygoid is present in 46421 and has been drawn by Woodward (1918 : pl. 17, fig. 4). The oral border bears about ten teeth; these are short and stout anteriorly, the posterior members of the row increasing in height.

When the animal is horizontal the quadrate articulation lies beneath the anterior border of the orbit, but if the skull is held with the parasphenoid horizontal, the articulation lies well in advance of the orbit. This follows because, owing to the deep trunk, the parasphenoid slopes ventrally from occiput to snout. Thus *Histionotus* has the smallest gape among macrosemiids. Although the quadrate and the remaining bones of the palate are poorly preserved, the quadratojugal is visible in P3614, and forms a long spine which lies along the upper edge of the preopercular as usual. It thickens anteriorly to form a stout rod behind the articular condyle of the quadrate. It is not clear whether the quadratojugal was fused to the quadrate at this point; in *H. oberndorferi* it is not fused.

(v) Dermal upper jaw. The premaxilla is partially preserved in 46421. The nasal process is much broader and stouter than in *Macrosemius* and appears to have extended beneath the frontals. The premaxillary teeth are slender and pointed.

The maxilla has a complex form, similar to that of *H. oberndorferi* (Fig. 35). The dorsal edge forms two shallow, smooth embayments; the oral border is concave and the hind edge convex. The maxilla appears to be toothless, although in some specimens (P577 for example) a few small pits are present along the posterior part of the oral border which may have held teeth. If present these must have been very small. A small foramen pierces the maxillary expansion in the anterior region.

(vi) Lower jaw. The mandible is badly crushed in the specimens; its component bones are more surely known in *H. oberndorferi.* The dentary teeth are styliform and very closely set. The facet for the quadrate condyle is very broad, deep and faces posteriorly.

(vii) Preopercular and opercular series. These are preserved in P577. The leading edge of the preopercular forms a regular curve from the skull roof to the jaw articulation; the greatest curvature occurs beneath the orbit. The trailing edge runs approximately parallel with the anterior border along the dorsal arm and forms an indentation at its base before continuing forward. The preopercular sensory canal communicated with the exterior through many narrow, dorsally-directed pores in the upper part of the bone, as in *Propterus*. Below this region, as usual, the canal was exposed by two or three large fenestrae and by a long ventral opening in the lower arm.

The opercular is about twice as deep as wide; its surface is completely covered by ganoine raised into a pattern of radiating ridges. The subopercular is wide and forms an ascending process along about half of the leading edge of the opercular. The dorsal border of the subopercular is deeply indented by the overlapping opercular. The surface of the subopercular is ornamented with ridges of ganoine. The interopercular is not fully exposed in the specimens; its form and size seem similar to those of other macrosemiid genera.

The uppermost two branchiostegals are visible on P577. The uppermost forms a broad blade extending along the entire ventral edges of the interopercular and subopercular. Unlike the condition of other members of the family, this ray, and to a lesser extent its predecessor, bears ganoine ridges.

(viii) Vertebral column. Several abdominal vertebrae are partially exposed in P3614. They form thick perichordal cylinders to which the neural and haemal arches are fused.

(ix) Pectoral girdle and fin. The post-temporals are preserved in P577. They resemble those of *Macrosemius* and *Propterus* in forming a broad triangular lamina medially and a short wide tube laterally around the lateral line. A few small patches of ganoine occur along the denticulated hind border (Fig. 33). The post-temporals are separated from each other by two large rectangular scales: these reduce the area of contact between the post-temporals and parietals. The surface of the two scales bears thick rugae of ganoine like those of the skull roof, unlike the even covering of ganoine on the trunk scales.

Part of the supracleithrum is visible in some specimens, but is poorly preserved. The upper part of the trailing edge is denticulated and bears ganoine. A large sensory pit is present, as in *Macrosemius*. The cleithrum is not exposed in the specimens.

The pectoral fin comprised at least ten rays. The leading ray is visible in P577; it is paired, each hemitrich bearing a row of sharply raised, elongated protuberances covered with ganoine. These are probably fringing fulcra which have fused to the ray. The postcleithral scales are described below, with the squamation.

(x) Pelvic fin. This consists of five rays, which are preceded by three large unpaired basal fulcra. Unlike in *Macrosemius* or *Propterus* the leading ray bears a series of very stout, closely-set fringing fulcra.

(xi) Dorsal and anal fins. The anal fin is not preserved; a few large fringing fulcra belonging to the fin are visible in P577. The anal fin of *H. oberndorferi* is better known.

Woodward (1918 : 79) estimated that the dorsal fin comprised about 25 rays which supported an uninterrupted fin-web. In *H. oberndorferi*, however, the dorsal fin is certainly divided. Woodward's drawing of Mansell-Pleydell's (1889) specimen of *H. angularis* suggests that the posterior 10 rays of the fin are longer than the first 15. This agrees with the condition in *H. oberndorferi*, in which the rays of the posterior lobe are longer than the last rays of the anterior lobe. In contrast with the latter species, however, all the dorsal rays are approximately equidistant from each other, so that there can have been no significant gap between the two lobes (if, as is assumed here, two lobes were present). The leading dorsal fin-ray is preceded by seven stout basal fulcra, and bears a series of large, deeply-overlapping fringing fulcra. The leading ray, not preserved distally in the specimens, was probably very long as in other species. The dorsal fin-rays all bear ganoine ridges on their lateral surfaces; this feature is not found in other macrosemiid genera.

(xii) Caudal fin. The caudal fin is deeply forked, with eight axial lobe rays and the usual eight rays below these. Paired fringing fulcra occur on the upper and lower edges of the fin. The axial lobe squamation is described below.

(xiii) Squamation. The three postcleithral scales are preserved in P577. The upper scale is very deep and extends along the greater part of the dorsal arm of the cleithrum; the lower two are much shorter. Both bear a complete layer of ganoine forming ridges similar to those on the opercular, and have smooth hind borders.

The trunk scales are deeper than broad; their posterior edges are slightly convex and bear denticulations (Woodward 1918 : pl. 17, fig. 5a). There are about 40 main lateral line scales and about 12 in the transverse row above the pelvic fins. The ganoine layer is smooth, forming slight ridges near the trailing edge which coincide with the denticulations. The scales in the ventral region between the paired fins are small and rounded; those between the pectoral fins bear tubercles and ridges of ganoine.

The lateral trunk scales form a narrow ridge on the inner surface as usual; the peg-and-socket is in alignment with the ridge (Woodward 1918 : pl. 17, fig. 5). Woodward (1918 : 79) reports that the main lateral line canal lay in a groove on the inner surface of the scale, although the canal was probably enclosed by a thin lateral wall as in *Macrosemius*. Approximately one-third of the main lateral line scales bear a small pit of the accessory lateral line. Similar pits, of the dorsal lateral line, occur on the scales alongside the dorsal fin. This region of the squamation displays several unusual features which are also found in *H. oberndorferi* and are described below.

The axial lobe of the caudal fin is covered by about seven rows of scales of which the lowermost continues into the uppermost fin-ray as usual.

Histionotus oberndorferi Wagner 1863

Figs 32, 35, 36

1863 *Histionotus oberndorferi* Wagner : 650; pl. 3.
1887 *Histionotus oberndorferi* Wagner; Zittel : 218, text-fig. 231.
1895 *Histionotus oberndorferi* Wagner; Woodward : 175.
1966 *Histionotus oberndorferi* Wagner; Schultze : 258, text-fig. 15.

Diagnosis. *Histionotus* reaching 200 mm standard length; mean proportions as percentage of standard length: head length 31%, trunk depth 40%, predorsal length 40%, prepelvic length 57%, preanal length 78%; dentary teeth stout, conical; dorsal fin lobes separated by a gap, and with a total of about 22 rays.

Holotype. Bayerische Staatssammlung für Paläontologie und historische Geologie, München, AS.19.1.

Horizon and Locality. Lower Kimmeridgian of the Kelheim region, Bavaria, Germany.

Material. Mü: AS.19.1, 1887.5.22.

Remarks. The proportions of the body of this species are almost identical to those of the type species, from which it differs in the shape of the dentary teeth. *H. oberndorferi* is extremely rare; the above two specimens are the only examples known, and further knowledge of the skull may eventually help to separate the two species more definitely. *Histionotus* has hitherto been thought to possess a single dorsal fin, but specimen 1887.5.22 shows clearly that it is divided.

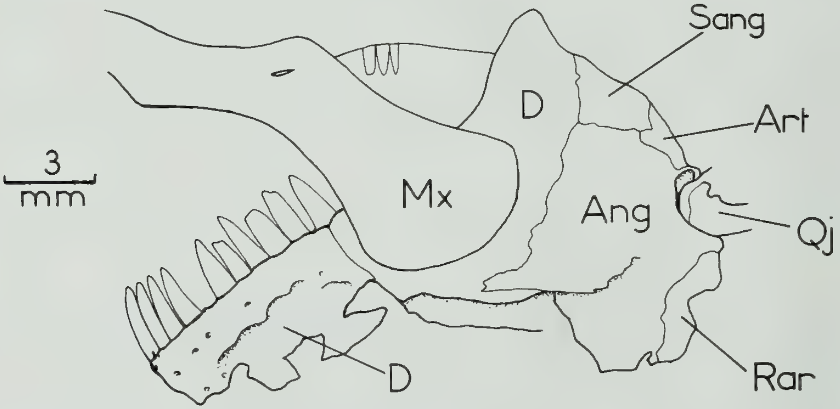

Fig. 35 *Histionotus oberndorferi* Wagner. Upper and lower jaws, as preserved in AS.19.1.

Description. (i) Skull. Details of the skull roof, preopercular, opercular and infraorbital series remain unknown. Fig. 36 was drawn from the impression of the skull in 1887.5.22, with details added from *H. angularis*.

The orbitosphenoid is preserved in AS.19.1 and in impression in 1887.5.22. This bone is very similar to that in *Propterus*; its hind margin is deeply emarginated, and it forms a large anterior lateral flange against which the eyeball presumably rotated.

As in the type species, the frontal forms vertical extensions which enwrap the preorbital region of the braincase; this feature is clearly displayed in AS.19.1. The maxilla is displayed in the type specimen (Fig. 35); it closely resembles that of *H. angularis*.

The dentary teeth are much broader and less tall than those of the type species; a row of ten is visible in AS.19.1. The oral border of the dentary rises steeply to form the pointed apex of the coronoid process (Fig. 35). The ventral border of the dentary forms a wide, open groove for the mandibular sensory canal as usual.

Two ossifications are visible on the hind border of the coronoid process. The larger, upper, element is the surangular and the lower the articular.

The angular is large; its suture with the dentary is approximately straight on the lateral surface of the coronoid process while above the sensory canal the angular forms the usual prolongation anteriorly. The deep posterior edge of the angular below the jaw articulation is capped by the retroarticular.

Of the palate only the quadrate is well known. The posterodorsal edge of this bone is rounded and just touches the metapterygoid. The articular condyle is broad, rounded and supported laterally by the quadratojugal, which is broad, tapering to a point immediately beyond the edge of the quadrate. The anterior head of the bone fits very closely against the quadrate behind the condyle, but no fusion is evident. As in *Propterus elongatus* a small notch occurs near the distal end of the quadratojugal. As in other macrosemiid genera, a lateral flange is present on the hyomandibular (AS.19.1).

(ii) Branchial arches. A few long, slender, pharyngeal teeth are exposed in the type specimen beneath the opercular. These contrast with the stout pharyngeal teeth known in *Macrosemius.*

(iii) Dorsal and anal fins. The anal fin is preserved in 1887.5.22. As in *Propterus* the fin-ray bases are closely set. The leading ray, which bears large fringing fulcra, is the longest, extending below the caudal fin; succeeding rays are progressively shorter.

The same specimen displays the dorsal fin, which is in two parts. The anterior part consists of about ten rays; it is high anteriorly, with a concave edge. The leading ray is very long, extending for a distance about equal to the depth of the trunk. It is closely followed by the second ray; the succeeding rays are more widely spaced. The anterior rays branch profusely so that the distal parts of the rays are formed entirely from thin filaments of bone. There are seven stout basal fulcra (Schultze 1966 : text-fig. 15) followed by long, deeply overlapping fringing fulcra which extend along the entire length of the leading ray.

The posterior dorsal lobe is composed of about 11 rays and is convex in outline; it is separated from the anterior part of the fin by a distance equal to the width of three scales.

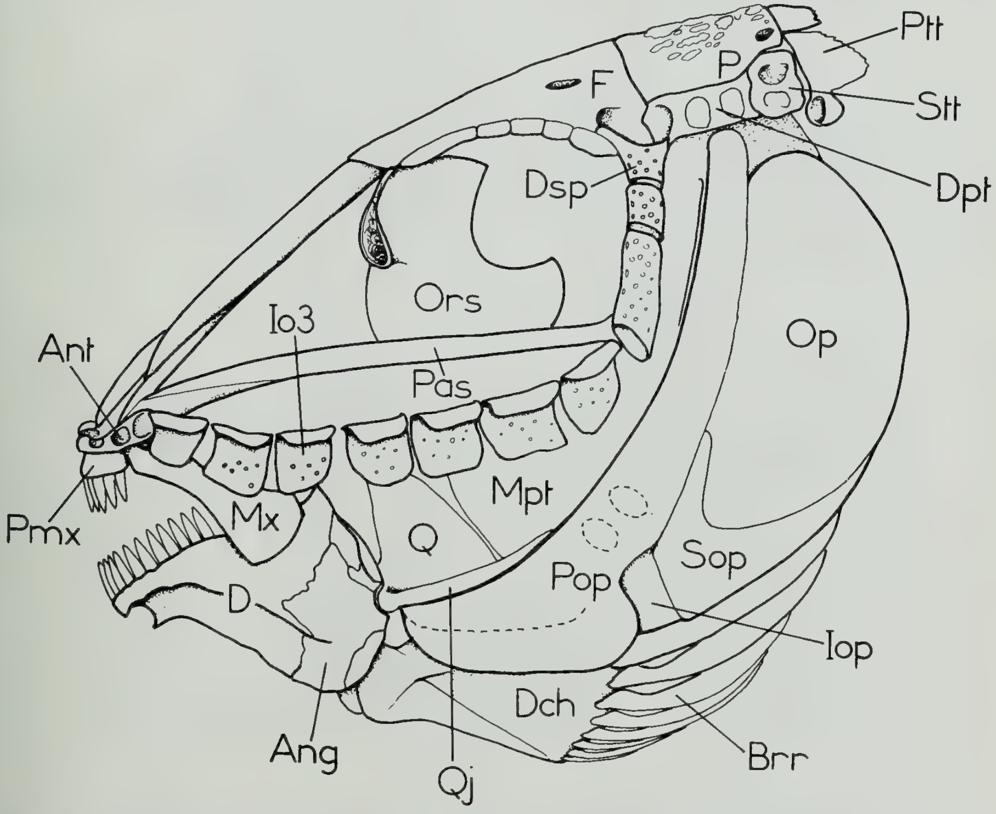

Fig. 36 *Histionotus oberndorferi* Wagner. Skull, with infraorbitals and roof restored from *H. angularis* Egerton. ×4½ approx.

(iv) Squamation. The trunk scales are similar in form, number and arrangement to those of the type species. The squamation flanking the dorsal fin of specimen AS.19.1 has been drawn and described by Schultze (1966 : 258, text-fig. 15). His observations and comments are repeated here.

The greater part of the dorsal fin is flanked by very deep scales some of which bear the pits of the dorsal lateral line on their surfaces. The lower part of the hind edges of these scales bear small pectinations, similar to those on the scales below them. The upper part of the scale, however, widens and the trailing edge of this region bears large pectinations. Beneath the basal fulcra of the dorsal fin, the uppermost longitudinal row is replaced by two rows, together equalling it in depth. The scales of the lower row, which bear the anterior pits of the dorsal lateral line, resemble the regular body scales, whereas those forming the upper row, alongside the fin, are small and taper posteriorly to form large pectinations. Schultze (1966 : 259) suggests that the row of deepened scales flanking the greater part of the length of the dorsal fin is the result of fusion between the small triangular scales and the regular longitudinal row which bears the dorsal lateral line.

Histionotus falsani Thiollière 1873

1873 *Histionotus falsani* Thiollière : 14; pl. 5, fig. 1.
1895 *Histionotus falsani* Thiollière; Woodward : 175.
1914 *Histionotus falsani* Thiollière; Eastman : 364; pl. 49, fig. 1.
1914 *Notagogus ornatus* Eastman : 366 (*partim*, specimen 4071 only).
1949 *Histionotus falsani* Thiollière; Saint-Seine : 208, fig. 92.

DIAGNOSIS. *Histionotus* reaching a standard length of about 150 mm; mean proportions as percentage of standard length: head length 32%, trunk depth 40%, predorsal length 39%, prepelvic length 60%, preanal length 81%; dentary teeth tall, conical.

HOLOTYPE. Muséum d'Histoire Naturelle, Lyon, 15.232.

HORIZON AND LOCALITY. Lower Kimmeridgian of Cerin, Ain, France.

MATERIAL. ML: 15.232, 15.239, 15.758; CM: 4071, 4077.

REMARKS. *H. falsani* is a rare, poorly known species. The fullest description is that given by Saint-Seine (1949 : 208, fig. 92) on which little improvement can be made while no specimens are available for acetic acid preparation. Although it does not appear to differ significantly from the type species in its proportions, the species is maintained here until more details of its structure become known.

Genus ***NOTAGOGUS*** Agassiz 1835

DIAGNOSIS. Small, fusiform macrosemiid fishes; skull-roof bones covered with an even layer of ganoine; sensory canals on skull of small diameter and completely enclosed in bone; fronto-parietal suture slightly sinuous; dermopterotic very large, housing the lateral part of the supratemporal commissure; supratemporal absent; supraorbitals forming one or two rows; dermosphenotic incorporated into skull roof; maxillary expansion asymmetrical, deep with straight oral border and convex upper and hind edges, maxillary teeth small, stout, forming a long row; dentary moderately curved, bearing small, stout teeth; anterodorsal edge of metapterygoid forming an acute angle; ectopterygoid bearing a row of small teeth; anterior border of preopercular forming a regular curve, ventral arm not greatly deepened, surface of opercular covered with a smooth layer of ganoine; pectoral fin with about 16 rays; pelvic fin comprising about six rays, fringing fulcra present; base of anal fin moderately extended, basal and fringing fulcra present; dorsal fin divided, each lobe with low convex profile; caudal fin with five or six axial lobe rays, weakly forked; squamation complete, forming a pattern of deepened hexagons, hind edges of scales pectinated, ganoine covering absent on ventral scales, which tend towards cycloidy; vertebral centra forming from dorsal and ventral crescents which fuse into complete cylinders in the anterior part of the trunk.

TYPE SPECIES. *Notagogus pentlandi* Agassiz (1835).

INTRODUCTION. The genus *Notagogus* was established by Agassiz (1835) to include four species

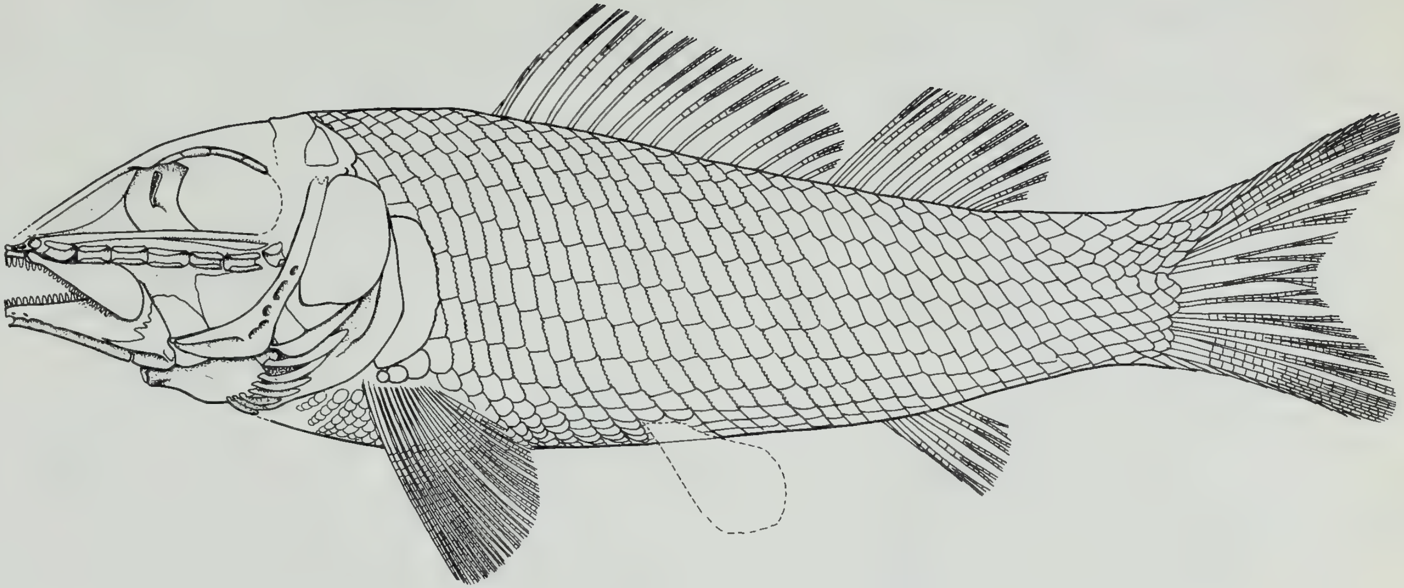

Fig. 37 *Notagogus denticulatus* Agassiz. Restoration of skeleton. × $1\frac{1}{2}$ approx.

of small fusiform fishes with divided dorsal fins. These were *N. zieteni* and *N. denticulatus* from the Lower Kimmeridgian of Bavaria, and *N. pentlandi* and *N. latior* from the Lower Cretaceous of Torre d'Orlando, Italy. Thiollière (1873) described *N. inimontis* and *N. margaritae* from the Lower Kimmeridgian of Cerin and Vetter (1881) added *N. macropterus*.

Woodward (1895) grouped several species, ascribed by Costa (1850, 1853, 1864) to various species of *Notagogus* and *Blenniomoeus*, in *N. pentlandi*. He also referred *N. latior* Agassiz to this species, and transferred *N. zieteni* to *Propterus microstomus*. A new species, *N. parvus* from the Wealden of Bernissart, was described by Traquair (1911), and Eastman (1914, 1917) added *N. decoratus* and *N. minutus* from Bavaria, and *N. ornatus* from Cerin, to the genus.

In his revision of the Cerin fishes, Saint-Seine (1949) gave a detailed account of *N. inimontis* Thiollière. Wenz (1964) published a preliminary description of *N. ferreri* from the Neocomian of Santa-Maria-de-Meya, Spain.

REMARKS. Thiollière (1850, 1873) drew and gave a short description of a small macrosemiid which he named *Macrosemius helenae*. Saint-Seine (1949) later gave a full description of this species, retaining it within that genus since he believed that the dorsal fin was single. In fact this species is synonymous with *N. margaritae* Thiollière (1858), which thus becomes *N. helenae* (Thiollière 1850).

N. macropterus Vetter (1881) belongs to *Propterus elongatus*, and the type specimen (CM 5114) of Eastman's (1914) *N. ornatus* belongs to *N. inimontis*. Eastman referred two other specimens to his *N. ornatus*; CM 4660 also belongs to *N. inimontis*, and CM 4071 is a specimen of *Histionotus falsani* Thiollière.

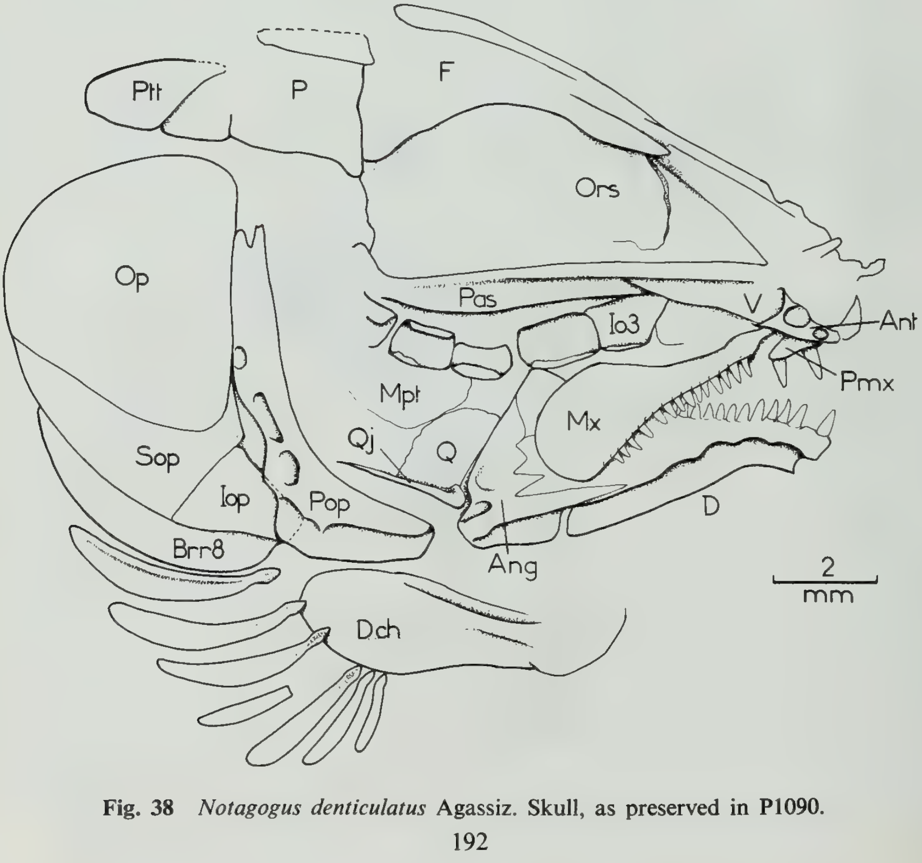

Fig. 38 *Notagogus denticulatus* Agassiz. Skull, as preserved in P1090.

Notagogus denticulatus Agassiz 1839

Figs 37–40

1839 *Notagogus denticulatus* Agassiz, **2** : pl. 50.
1844 *Notagogus denticulatus* Agassiz, **2**, 1 : 294; 2 : 289.
1851 *Notagogus denticulatus* Agassiz; Wagner : 65.
1863 *Propterus denticulatus* (Agassiz) Wagner : 646.
1881 *Notagogus denticulctus* Agassiz; Vetter : 43.
1895 *Notagogus denticulatus* Agassiz; Woodward : 187.
1917 *Notagogus minutus* Eastman : 287; pl. 14, fig. 4.

DIAGNOSIS. *Notagogus* reaching standard length of 70 mm; mean proportions as percentage of standard length: head length 33%, trunk depth 29%, predorsal length 41%; dorsal fin-ray count: ant. 10–14, post. 10–11; about 34 lateral line scales, only part of their hind borders bearing prominent serrations; no free fulcra on pectoral fin, very few fringing fulcra on first dorsal fin, fringing fulcra on anal fin.

HOLOTYPE. Bayerische Staatssammlung für Paläontologie und historische Geologie, München, AS.1.768.

HORIZON AND LOCALITIES. Lower Kimmeridgian of Eichstätt and Kelheim regions of Bavaria, Germany.

MATERIAL. BM(NH): P1090, P1089, P3610-11; Mü: AS.1.768; Ei: E1937-70; DM: S43 (photograph only examined).

DESCRIPTION. (i) General. *N. denticulatus* has the small size and regularly fusiform body typical of the genus. Proportional measurements, based upon three of the specimens, are given above. The following account applies largely to P1090, an immature specimen developed in acetic acid (Fig. 38).

(ii) Skull-roof and braincase. The structures are poorly preserved in the specimens; those of *N. helenae* and *N. inimontis* are described below (pp. 196–8, 200).

(iii) Circumorbital series. The supraorbitals remain unknown. The antorbital forms the usual tapering tube around the anterior part of the infraorbital sensory canal (Fig. 38). Two large pores in the lateral wall are visible. Infraorbitals 3–7 are present in the specimen. These form delicate scrolls around the upper and lower borders of the infraorbital sensory canal; they are perforated by fine pores. The last two infraorbitals, behind the eye, are not preserved.

(iv) Hyopalatine bones. The quadrate and the lower part of the metapterygoid are visible; both have corrugated surfaces. These two bones, and the quadratojugal, are better known in *N. inimontis*.

(v) Dermal upper jaw. Two of the tall, conical premaxillary teeth are visible (Fig. 38). The remainder of the premaxilla remains unknown.

The maxilla forms a slender cylindrical shaft behind the medial process. The ventral surface of the shaft is raised into a bulge. The dorsal border is convex and continues into the rounded hind border of the bone. The oral border is slightly concave and bears about 15 small, stout teeth which extend onto the cylindrical part of the maxilla; the teeth increase in height anteriorly.

(vi) Lower jaw. The mandible in this genus is long, extending about half of the length of the skull. The coronoid process is broad and shallow and the curvature of the ventral border of the dentary is less marked than it is in other macrosemiid genera.

The mandibular sensory canal entered the angular below a slender arch of bone as in *Propterus*. It continued forward, as usual, through a wide trough along the ventral parts of the angular and dentary.

The angular extends along the lower half of the posterior border of the coronoid process. The surangular appears to form the greater part of the dermal coronoid process, although most of the bone is hidden by the maxilla in the specimen and its complete outline cannot be followed. The suture between the dentary and angular follows a long zigzag course, the angular forming a long tapering process anteriorly along the dorsal edge of the sensory canal as usual. The dentary

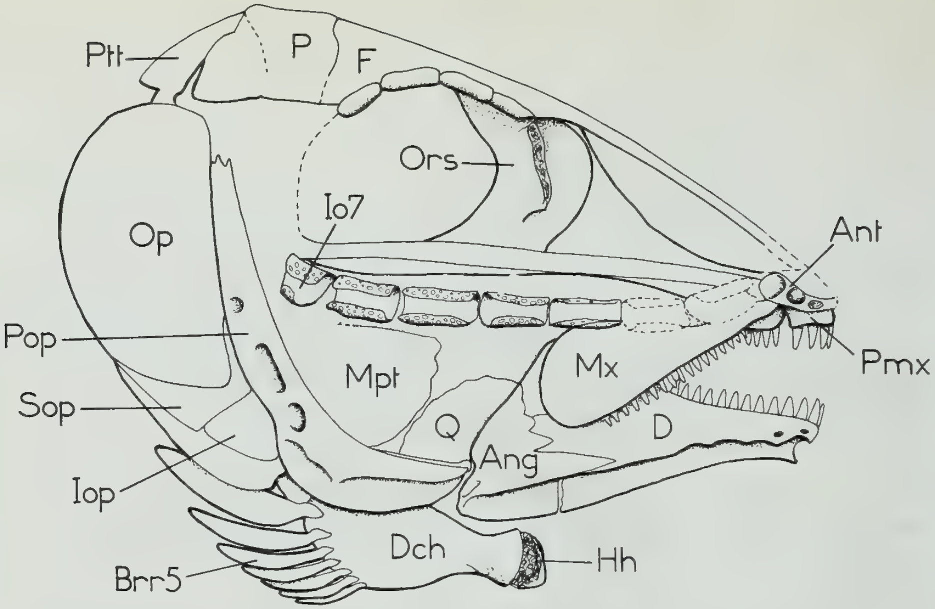

Fig. 39 *Notagogus denticulatus* Agassiz. Restoration of skull. × 6 approx.

bears a row of about 12 closely-set teeth intermediate in size between those of the maxilla and premaxilla.

(vii) Preopercular, hyoid arch and branchiostegal series. The anterior edge of the preopercular forms a smooth curve. The dorsal arm falls short of the skull-roof and the ventral arm ends at the level of the quadrate articulation as usual. As in other macrosemiids the preopercular sensory canal was exposed by two large fenestrae in the lower part of the upper arm. The ventral arm too has the typical macrosemiid form (Fig. 38).

The opercular is as deep as it is broad in the young specimen (P1090); in older specimens it becomes proportionally narrower. The subopercular is large and deeply embayed along the suture with the opercular. The suture between the subopercular and interopercular is long and straight as usual. The anterior end of the latter is remote from the mandible as in all other members of the family. The hyomandibular is not exposed in the specimens.

The proximal ceratohyal is partially visible in P1090; it is less deep posteriorly than it is in other macrosemiids. This specimen also displays the eight branchiostegal rays; these are similar in form and arrangement to those of *Macrosemius*. The blade of the uppermost ray is deeper than those of the remainder and appears to have been attached to the operculum and not to have articulated with the ceratohyal.

(viii) Vertebral column. The axial skeleton remains unknown in this species; it is described in other members of the genus below.

(ix) Pectoral girdle and fin. The pectoral girdle is not clearly preserved in the specimens. It seems to resemble that of *N. helenae* described below.

The fin consists of about 15 rays. The leading ray, compound in origin, is well preserved in P1090 (Fig. 40A), and is formed mainly from a long unfused pair of branching, segmented hemitrichs resembling those of the succeeding rays. The basal part of the dorsal hemitrich is produced into a short basal process, and appears to be fused to the endoskeletal propterygium. A shorter ray, also with a dorsal process, is fused along one-third of the unsegmented part of the major lepidotrich, its sharp tip projecting freely. Two small spines occur above this point on the major ray; these are probably fused fringing fulcra.

(x) Pelvic fin. The fin was supported by at least four rays, of which the first is preceded by basal and fringing fulcra.

(xi) Dorsal and anal fins. The dorsal fin is divided into two lobes of approximately equal height; this contrasts with the condition in *Histionotus* and *Propterus* where the anterior lobe is the taller. There are about 14 anterior rays preceded by three basal and about one fringing fulcrum. The last three rays of the lobe decrease rapidly in height to form a rounded hind border. The posterior lobe comprises nine or ten rays, more closely set than those of the anterior part. All the dorsal fin-rays are segmented and branch once.

The anal fin consists of about four rays, the first bearing fringing fulcra. None of the rays is markedly long, and the base of the fin is not compact, in contrast to the condition in *Propterus* and *Histionotus*.

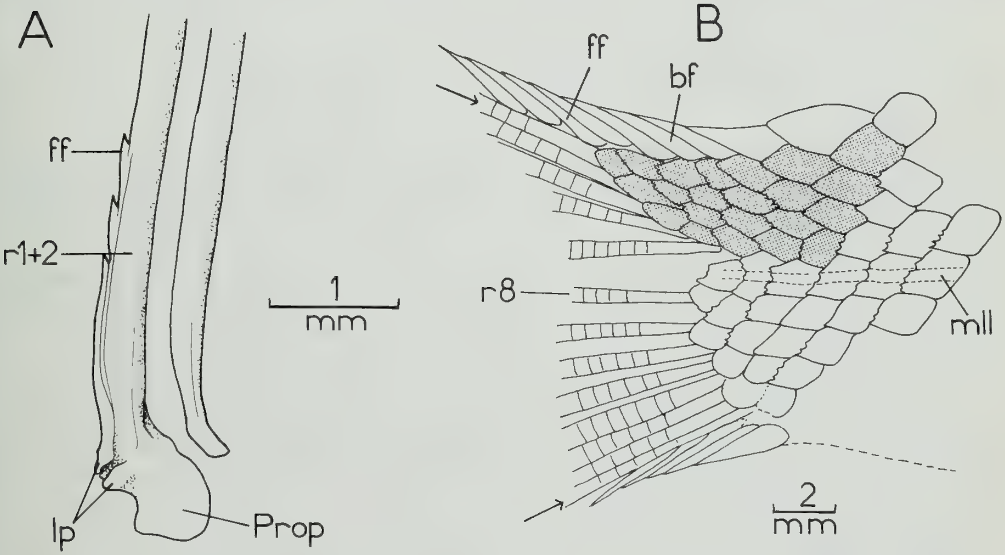

Fig. 40 *Notagogus denticulatus* Agassiz. A, leading rays of right pectoral fin of P1090. B, caudal squamation, as preserved in AS.1.768, axial lobe shaded. Arrows indicate outermost fin-rays.

(xii) Caudal fin. This is preserved in AS.1.768; it is weakly forked. The axial lobe bears five rays; as usual eight rays occur below these. As in *Propterus* and *Histionotus* the axial lobe rays supported the upper lobe of the fin. Both leading edges of the fin bear fringing fulcra. The axial lobe squamation is shown in Fig. 40B.

(xiii) Squamation. There are four postcleithral scales; the uppermost is very deep, extending along the dorsal arm of the cleithrum. The remaining three lie in a row above the insertion of the pectoral fin; they are small, circular and decrease in size anteriorly.

There are about 34 lateral line scales, and about 14 scales in the transverse rows in the anterior part of the body. The prominent serrations on the posterior edges of the scales are restricted to the part overlapping the succeeding scale in the same longitudinal row. Thus in the deepest scales, behind the skull, about one-fifth of the hind border is smooth.

In the ventral region between the pectoral fins the scales form a cycloid pattern similar to that described in *Propterus microstomus* (AS.1.768).

Notagogus helenae (Thiollière 1850)

Fig. 41

1850 *Macrosemius helenae* Thiollière : 135.
1858 *Notagogus margaritae* Thiollière : 783.
1873 *Macrosemius helenae* Thiollière; Thiollière : 14; pl. 6, fig. 2.
1873 *Notagogus margaritae* Thiollière; Thiollière : pl. 6, fig. 4.
1883 *Macrosemius helenae* Thiollière; Sauvage : 478.
1949 *Macrosemius helenae* Thiollière; Saint-Seine : 193, text-figs 84–86; pl. 20B, C.

DIAGNOSIS. *Notagogus* reaching 100 mm standard length; mean proportions as percentage of standard length: head length 32%, trunk depth 28%, predorsal length 33%; dorsal fin-ray counts: ant. 15, post. 10–12; about 38 lateral line scales, their entire hind borders bearing small serrations; two lobes of dorsal fin closely spaced; fringing fulcra on anal and caudal fins only.

HOLOTYPE. Muséum d'Histoire Naturelle, Lyon, 15.220.

HORIZON AND LOCALITY. Lower Kimmeridgian of Cerin, Ain, France.

MATERIAL. LM: 15.208, 15.220, 15.223, 15.224, 15.230, 15.231, 150.752, 150.875, 15.406, 150.756; L: AC.1874-543.

REMARKS. Thiollière (1850) named two small species of macrosemiid from Cerin, *Macrosemius helenae* and *Notagogus inimontis*. In his posthumous publication of 1873 there were lithographs of these two species (pl. 6, figs 2, 3), and of another of similar shape and size, *N. margaritae* (pl. 6, fig. 4). He left no description of the latter.

Thiollière and later Saint-Seine (1949) maintained that *M. helenae* possessed a long, undivided dorsal fin and hence was correctly ascribed to this genus, but there are several points of dissimilarity between *M. helenae* and the type species of *Macrosemius* which call this observation into question. Thus *M. helenae* differs from *M. rostratus* in having, for example, a forked caudal fin, a complete covering of scales with no intervening scale-rows and a full row of maxillary teeth.

Thiollière's *M. helenae* greatly resembles *Notagogus margaritae* in form and size and in the total number of dorsal fin-rays (about 26). Saint-Seine (1949 : 204) maintained that the dorsal fins of Thiollière's specimens of *N. margaritae* were single, and thus transferred them to *M. helenae*. However, the full outline of the dorsal fins of these two species is seldom preserved; usually only the unsegmented proximal parts of the rays have survived. Since the rays exhibit an even width throughout the length of the fin, it is difficult to ascertain whether the fin was divided or not if the two lobes were placed close together.

Re-examination of the specimens has shown that in fact those referred to *M. helenae* by Saint-Seine possess divided dorsal fins and are wrongly ascribed to *Macrosemius*. Thus in 15.223 and 15.224 (included by Thiollière in *N. margaritae*) there is a slight change in inclination between the 15th and 16th dorsal fin-rays indicating that the two rays belonged to separate fin webs, although there is no appreciable change in the spacing between them. In the other four specimens listed by Saint-Seine (1949 : 194), the bases lie flat. In 150.756 too there is a change in inclination between the 15th and 16th rays, and in 150.875, an immature specimen of 25 mm standard length, in which the full outline of the fin is preserved, there is unquestionably a separate anterior lobe supported by 15 rays.

Thus the specimens listed above are here taken to belong to *N. helenae*; all of them possess 15 anterior dorsal fin-rays and between 10 and 12 posterior dorsal fin-rays. This species differs from the type species *N. pentlandi* in possessing a greater number of dorsal fin-rays, a smaller predorsal length and a more obtuse snout profile.

DESCRIPTION. (i) Skull roof and braincase. The state of preservation of the material has led to several inaccuracies in the description given by Saint-Seine (1949 : 193–199). A full redescription is given below.

The sensory canals of *Notagogus* differ from those of other macrosemiids in being comparatively narrow; they are completely surrounded by bone and not exposed by large fenestrae.

Saint-Seine (1949 : fig. 84) misunderstood the structure of the preorbital region of the frontals; he considered that these ended above the front of the orbit and that the ethmoidal region was devoid of a dermal bone covering. In fact the frontals form the usual trough for the supraorbital sensory canal in this region. There is no sound evidence, either, for the kidney-shaped nasals of Saint-Seine's description.

The parietals are large, roughly triangular bones. The anterior border, which corresponds to the greatest width, is overlapped by the frontal along a slightly sinuous suture. The anterolateral border of the parietal forms a short suture with the dermosphenotic. The posterolateral border forms two large embayments as it converges towards the midline; in contrast with other members of the family, the parietal enclosed only a very short section of the supratemporal commissure on either side of the midline. The surface of the bone is covered with an even layer of ganoine which is interrupted by the anterior and middle pit-lines. The middle pit-line forms a short groove close to, and parallel with, the posterior edge of the parietal. The anterior pit-line is equally short, extending at an angle of about 100 degrees anterolateral to the middle pit-line (Fig. 41). There is no evidence to suggest that a branch of the supraorbital sensory canal extended onto the parietal (cf. Saint-Seine 1949 : fig. 84).

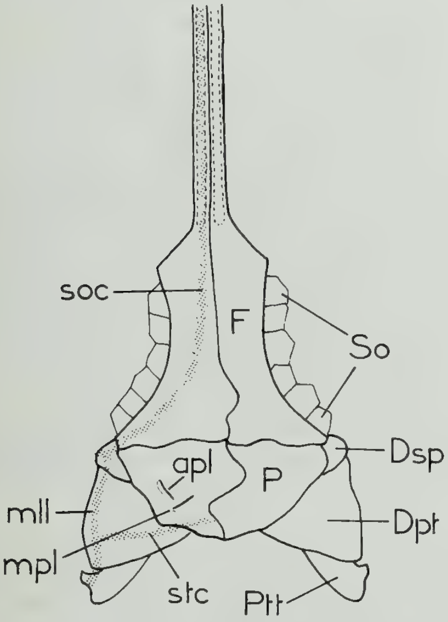

Fig. 41 *Notagogus helenae* (Thiollière). Skull roof, as preserved in 15.220. ×6.

Saint-Seine (1949) identified two bones in contact with the posterolateral border of the parietal: a 'supratemporal' (i.e. dermopterotic) suturing with the anterior embayment, and an 'extrascapular' (i.e. supratemporal) posteriorly. This region of the skull, however, is in fact occupied by a single, large, triangular bone; Saint-Seine has mistaken for a suture the collapsed tube of the lateral part of the supratemporal commissure which passed through this element. This condition is unknown in other macrosemiids. Since this bone houses both the supratemporal commissure and the cephalic division of the main lateral line, it could be the dermopterotic, the supratemporal, or the result of the fusion of both. The supratemporal is reduced in all macrosemiids and may have disappeared in *Notagogus*, its place and sensory canal taken by the dermopterotic. Alternatively, since fusion has perhaps occurred between the parietal and the medial supratemporal (see p. 143), fusion between the lateral supratemporal and the dermopterotic may have occurred also. The bone is labelled dermopterotic in Fig. 41.

The dermosphenotic is described here since it is fully incorporated into the skull-roof, unlike its condition in other members of the family. It forms a short posteromedially-directed process between the dermopterotic and parietal. Although the full outline of the bone is not exposed in the specimens, the bone clearly enclosed the point of fusion between the infra- and supraorbital sensory canals.

The parasphenoid is, as usual, stout and straight. A small basipterygoid process is visible beneath the ascending process of the parasphenoid in 15.220. A shallow groove, which, as Saint-Seine suggested (1949 : 196), may have held the efferent pseudobranchial artery, passes along the bone above the basipterygoid process.

A large orbitosphenoid surmounts the parasphenoid about midway along its length. Its posterior edge is deeply concave and a lateral flange projects laterally along the anterior limit of the orbit, as in *Propterus* and *Macrosemius*. The anterior border of the bone is straight and vertical.

(ii) Circumorbital series. Unlike the condition in other members of the family, there appear to be two rows of supraorbitals. These are small and polygonal in shape, as described by Saint-Seine (1949 : 194, fig. 85).

The remains of infraorbitals 2–7 are preserved in 15.223; they are of similar shape and size to those of *Notagogus denticulatus* and Saint-Seine's (1949 : 196, fig. 85) identification of three large infraorbital plates was mistaken. Also there is no evidence to indicate that the sclerotic was ossified.

(iii) Hyopalatine bones. The palate is exposed in 15.220. The straight edges of the indentation in the anterodorsal border of the metapterygoid form an angle of about 70 degrees; this contrasts with the condition in *Macrosemius* and *Propterus* where this angle is obtuse. The anteroventral border of the metapterygoid forms a long straight suture with the quadrate.

The anteroventral border of the quadrate is excluded from the oral border of the palate as usual by a long extension of the ectopterygoid which reaches almost to the jaw articulation (Saint-Seine 1949 : 196, fig. 85). The ectopterygoid bears a long row of very small hemispherical teeth along its thickened oral border. The endopterygoid forms a long gently curving suture with the ectopterygoid, its medial edge lying alongside the parasphenoid.

The relationship between the quadrate and the quadratojugal is more certainly known in *N. inimontis*, described below.

(iv) Dermal upper jaw. The maxilla resembles that of *N. denticulatus* in having a ventral thickening on the shaft and in the form of the posterior expansion (15.223). The teeth, however, are fewer, and are restricted to the maxillary expansion.

The premaxilla is visible in 15.220. The nasal process is long and stout, and contacts the dorsal surface of the braincase. The dentigerous head of the bone bears about four stout tapering teeth, each about four times the size of those on the maxilla.

(v) Lower jaw. The posterior edge of the coronoid process arises much more steeply than does that of *N. denticulatus* (15.208). The dentary supports about ten teeth, slightly larger than those on the premaxilla. The greater part of the dermal coronoid process is formed by the dentary; this bone forms a long suture with the angular, curving anteroventrally. The surangular remains unknown. The region of the mandible enclosing the sensory canal is not preserved in the specimens.

(vi) Preopercular, hyoid arch and opercular series. The preopercular is crescent-shaped, with the dorsal arm slightly longer than the ventral arm. The latter is not as deep as that of *N. denticulatus*. At least two fenestrae are present in the lateral wall of the sensory canal in the region of the greatest curvature of the bone (15.208).

The opercular (15.220) is deeper than broad, with a smoothly curved trailing edge. The subopercular is similar to that of *N. denticulatus*; it forms a straight suture with the interopercular which as usual is small and, contrary to the opinion of Saint-Seine (1949 : 197), does not resemble a branchiostegal ray.

There are seven or eight branchiostegals, similar to those of *N. denticulatus*.

(vii) Vertebral column. The feebly-ossified vertebral column has been described by Saint-Seine (1949 : 198, fig. 86) in specimens 15.231 and AC 1874-543. In the abdominal region there are large, crescentic, dorsal and ventral hemicentra; each dorsal hemicentrum is in contact with, and slightly in advance of, its ventral partner. The neural and haemal arches rested on the notochord in the gaps between the hemicentra. The ventral crescents decrease in size in the caudal region and the bases of the haemal arches enlarge and spread around the notochord. The neural arches are paired as usual but do not articulate with the proximal dorsal fin radials as suggested by Saint-Seine (1949 : 198).

(viii) Pectoral girdle and fin. The post-temporal is of the usual triangular shape, with a broad canal in the lateral border which housed the main lateral line. The supracleithrum is large and forms a wide, anterodorsally-facing, funnel-shaped opening for the exit of this canal. The cleithrum is a broad, gently curving bone; it is wider than that drawn by Saint-Seine (1949 : fig. 85) since it comprises the piece he mistook for an anterior postcleithral scale. The anterior and posterior borders of the cleithrum are smoothly convex. Two vertical rows of denticles are present on the lateral surface.

The endoskeleton of the fin remains unknown. There are at least 10 pectoral fin-rays; no fringing fulcra are preserved.

(ix) Pelvic fin. The pelvic fin consists of five rays; no fringing fulcra are present.

(x) Dorsal and anal fins. As discussed above, the dorsal fin is divided, contrary to the views of Thiollière (1873) and Saint-Seine (1949 : 199). The total number of dorsal fin-rays, about 26, is high for this genus. The anterior lobe is the longer, with 15 rays. The leading ray is preceded by two short basal fulcra; there are no fringing fulcra. The posterior lobe follows very closely behind the first, and both lobes are low and rectangular in outline. The dorsal fin radials are similar to those described in *Macrosemius* (15.231).

The anal fin is poorly preserved in the specimens; it is formed from five rays, of which the first bears fringing fulcra.

(xi) Caudal fin. The caudal fin comprises 14 rays, of which six emanate from the axial lobe. The axial lobe rays follow the typical macrosemiid pattern: the uppermost is continuous with the longest scale row, the following rays clasp the hypurals, and the lowermost, slightly separated from the others, clasps the tip of its hypural. Both leading edges of the fin bear fringing fulcra.

(xii) Squamation. There are about 36 lateral line scales and 11 in the deepest transverse row. The hind borders of the flank scales are convex and, in contrast to the condition in *N. denticulatus*, bear serrations along their entire length. The ventral scales, between the paired fins, are cycloid (15.231).

There are four postcleithral scales, decreasing in depth ventrally; their hind borders are smooth. The large anterior postcleithral scale drawn by Saint-Seine (1949 : fig. 85) is in fact part of the cleithrum, as explained above.

Notagogus inimontis Thiollière 1850

Fig. 42

1850 *Notagogus Imi montis* Thiollière : 137.
1858 *Notagogus iunismontis* Thiollière : 783 (name only).
1873 *Notagogus inimontis* Thiollière; Thiollière : 15; pl. 6, fig. 3.
1893 *Notagogus inimontis* Thiollière; Sauvage : 428.
1895 *Notagogus inimontis* Thiollière; Woodward : 188.
1914 *Notagogus inimontis* Thiollière; Eastman : 365; pl. 49, fig. 2; pl. 50, figs 1, 2.
1914 *Notagogus ornatus* Eastman : 366; pl. 50, fig. 3 (*partim*, specimens 5114, 4660 only).
1949 *Notagogus inimontis* Thiollière; Saint-Seine : 205, text-figs 90, 91.

DIAGNOSIS. *Notagogus* reaching standard length of 90 mm; mean proportions as percentage of standard length: head length 36%, trunk depth 27%, predorsal length 43%; dorsal fin-ray count: ant. 10–13, post. 10; about 34 lateral line scales, their entire borders bearing small serrations; all fins bearing fringing fulcra.

HOLOTYPE. Muséum d'Histoire Naturelle, Lyon, 15.242.

HORIZON AND LOCALITY. Lower Kimmeridgian of Cerin, Ain, France.

MATERIAL. LM: 15.420, 15.416, 15.242, 15.250, 15.249, 15.409; CM: 5114, 5115, 5116, 4418, 4654.

REMARKS. This species bears a strong resemblance to *N. denticulatus* in its body proportions and fins. Nevertheless it is not always easy to distinguish from *N. helenae* in the Cerin fauna, and thus the dissimilarities between these two are stressed below.

DESCRIPTION. (i) Skull-roof and braincase. The skull-roof is very similar to that of *N. helenae* (Saint-Seine 1949 : fig. 90); it is displayed in 15.249. Saint-Seine thought, wrongly, that the frontals did not extend laterally over the sides of the ethmoidal region; in fact they do so, as in *Histionotus*.

As in *N. helenae* the parietal is flanked by a single large bone which Saint-Seine, probably correctly, identified as the 'supratemporal' (= dermopterotic). There is no evidence to support the presence of a narrow bone identified as the 'extrascapular' (= supratemporal) by Saint-Seine (1949 : figs 90, 91).

The dermosphenotic is fully incorporated into the skull roof as in *N. helenae* (CM 5114). The infraorbital sensory canal entered the bone through a ventrally-directed pore and joined the supratemporal canal within it.

(ii) Circumorbital bones. A single row of four small polygonal supraorbitals is present along the orbital embayment of the frontals (Saint-Seine 1949 : figs 90, 91). The infraorbitals are not preserved in any of the specimens.

(iii) Hyopalatine bones. The metapterygoid and quadrate are visible in CM 5114, and are very similar to those of *N. helenae*. The quadrate articulation with the mandible is stout and deep. The quadratojugal lies in its usual position along the upper edge of the preopercular (Fig. 42). Anteriorly the bone forms a stout rod fitting closely behind the ventrolateral part of the quadrate condyle; no fusion between the two bones is evident, although it may have occurred. The posterior part of the bone is, unusually, expanded over the ventrolateral surface of the metapterygoid.

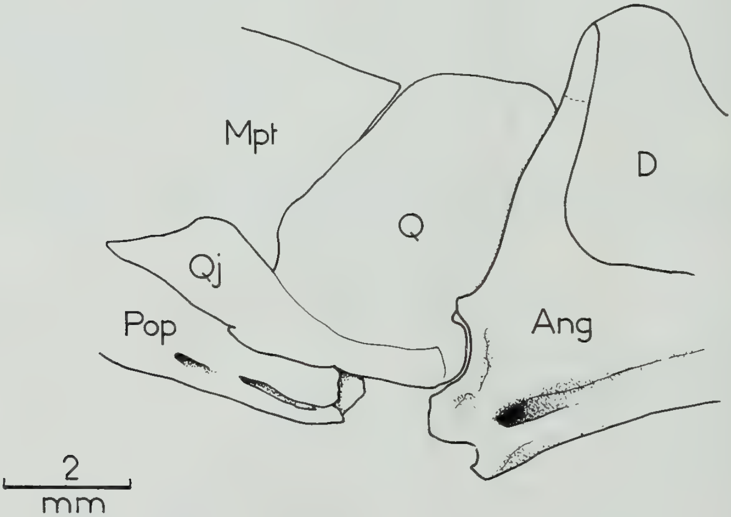

Fig. 42 *Notagogus inimontis* Thiollière. Region of right jaw articulation of CM 5114.

(iv) Dermal upper jaw. The premaxilla bears several stout teeth. The lower part of the nasal process is visible in 15.249, as Saint-Seine noted (1949 : 206, fig. 91).

The posterior expansion of the maxilla is deeper than that of *N. helenae*. The oral border is straight and bears more teeth (about 20) than that of *N. helenae*, extending onto the anterior, cylindrical part of the bone. The teeth are small and peg-like (15.416).

(v) Lower jaw. The mandible, preserved in 15.416 and CM 5114, closely resembles that of *N. helenae*.

(vi) Preopercular, hyoid arch and opercular series. The anterior edge of the preopercular forms a regular arc from the skull-roof to the jaw articulation (CM 5114); it is not sharply bent as described by Saint-Seine (1949 : fig. 91). Two fenestrae occur in the canal in the lower part of the dorsal arm as usual (15.242).

The opercular is deeper than broad, with a smoothly rounded trailing edge (cf. Saint-Seine 1949 : fig. 91); its surface is covered by an even film of ganoine. The remaining opercular and branchiostegal bones, as far as can be determined from the specimens, resemble those of *N. denticulatus*.

The distal ceratohyal is exposed in several specimens. It is thickened dorsally, becoming very stout as it tapers anteriorly. It forms a thin ventral expansion for the articulation of the branchiostegals, as usual.

(vii) Vertebral column. The vertebrae are exposed in a small specimen (CM 5115) of standard length 70 mm. These form complete cylinders in the abdominal region. Where the smooth outer surfaces of the centra have been removed, vertical, fibrous striations are exposed; these indicate that the larger part of the centra was formed of ossification in the notochordal sheath.

(viii) Pectoral girdle and fin. The dermal pectoral girdle is not clearly exposed in any of the specimens. It appears to resemble that of *N. helenae*.

There are six proximal pectoral radials; the sixth, the longest, bears lateral flanges, as in *Macrosemius rostratus* (15.409). The fin comprises 17 rays, the leading ray bearing free fringing fulcra, in contrast to that of *N. denticulatus* (15.416, 15.242).

(ix) Pelvic girdle and fin. The pelvic basipterygium is preserved in 15.409; it is similar in shape to that of *Macrosemius*. Eight pelvic rays are visible in 15.249. The leading ray is preceded by three basal fulcra and bears fringing fulcra.

(x) Dorsal and anal fins. The dorsal fin of this species resembles that of *N. denticulatus* both in form and in the number of fin-rays. The anterior lobe of the fin, with about 12 rays, is about twice as long as the posterior part, in which the 10 rays are less widely spaced. Although the gap between the lobes is small, the discontinuity between them is obvious since the last rays in the anterior lobe are short and thin compared with those of the posterior lobe. This contrasts with the condition in *N. helenae* in which the rays are uniform throughout the two lobes. Also in contrast to *N. helenae* and *N. denticulatus*, the three basal fulcra at the base of the leading ray are followed by fringing fulcra, and the first ray of the posterior lobe is unsegmented, unbranched and much shorter than its successors.

The anal fin is composed of about five rays preceded by three unpaired basal fulcra and a series of deeply imbricated fringing fulcra.

(xi) Caudal fin. The caudal fin does not differ significantly from those of the other species of *Notagogus* described above.

(xii) Squamation. There are three postcleithral scales aligned in tandem along the posterior border of the cleithrum; the uppermost is largest and they decrease in size ventrally. Their hind borders are smooth.

There are about 34 lateral line scales and about 11 transverse scales at the deepest point of the trunk; the main lateral line passed through the fifth row from the dorsal midline. The hind border of the flank scales is serrated. The longitudinal row alongside the dorsal fin bears the pits of the dorsal lateral line on several of its scales, as in *Histionotus*.

The ventral squamation, cycloid as in other species of *Notagogus*, is exposed in CM 5114.

Notagogus pentlandi Agassiz 1835

1835 *Notagogus pentlandi* Agassiz **2** : pl. 49, fig. 2.
1835 *Notagogus latior* Agassiz **2** : pl. 49, fig. 3.
1844 *Notagogus pentlandi* Agassiz **2**, 1 : 10, 294.
1844 *Notagogus latior* Agassiz **2**, 1 : 10, 294.
1850 *Notagogus pentlandi* Agassiz; Costa : 312; pl. 5, fig. 2; pl. 7, fig. 5.
1850 *Notagogus erythrolepis* Costa : 314; pl. 4, figs 6, 7.

1850 *Notagogus minor* Costa : 315; pl. 5, fig. 4.
1850 *Blenniomoeus longicauda* Costa : 319; pl. 6, fig. 2.
1850 *Blenniomoeus brevicauda* Costa : 321; pl. 5, fig. 3.
1853 *Blenniomoeus major* Costa : 34; pl. 2, figs 4–6.
1864 *Notagogus pentlandi* Agassiz; Costa : 72; pl. 12, fig. 5.
1864 *Notagogus crassicauda* Costa : 74; pl. 12, figs 6, 7.
1864 *Blenniomoeus longicauda* Costa; Costa : 99.
1864 *Notagogus erythrolepis* Costa; Costa : 102; pl. 11, fig. 11.
1864 *Notagogus gracilis* Costa : 103; pl. 11, fig. 8.
1882 *Notagogus pentlandi* Agassiz; Bassani : 237, 239.
1895 *Notagogus pentlandi* Agassiz; Woodward : 186; pl. 3, figs 7, 8.

DIAGNOSIS. *Notagogus* reaching standard length of 115 mm; mean proportions as percentage of standard length: head length 36%, trunk depth 27%, predorsal length 45%; dorsal fin-ray count: ant. 14, post. 10; about 34 lateral line scales.

HOLOTYPE. British Museum (Natural History), 117.

HORIZON AND LOCALITY. Lower Cretaceous (Albian or Aptian) of Torre d'Orlando, Naples, Italy.

MATERIAL. BM(NH): 117, P2065, P6866, P1097a, b, c.

REMARKS. The available specimens reveal little detail, since the bones are largely shattered beyond recognition. This species is closely similar in fin form and body proportions to *N. denticulatus*, but until the squamation and fin fulcra are more fully known it seems reasonable to maintain the two species as separate, in view of their separation in time.

Three of the specimens (P1097a, b, c) are very small and there is no guarantee that they belong to *N. pentlandi*. They probably do, however, as the proportions of the head and the long dorsal fin differentiate them from other members of the Torre d'Orlando fauna.

DESCRIPTION. (i) Caudal fin. The adult condition is preserved in P2065. There are 14 rays of which six emerge from the axial lobe. The internal skeleton of the fin is shown in two of the juvenile specimens, P1097a (SL 44 mm) and P1097b (SL 54 mm). In P1097a, six supports articulated with six full-length ventral rays. Another two smaller, unsegmented rays occur below these, as in *Enchelyolepis*. These two rays would presumably have elongated to form the adult complement of eight lower rays. The condition in P1097b is similar; in both these specimens there are only four axial lobe rays.

(ii) Vertebral column. The axial skeleton is exposed in P1097c; it has been drawn by Woodward (1895 : pl. 3, fig. 8). In the caudal region each vertebral unit consists of a ventral crescent, fused to the haemal arch, and a dorsal crescent alongside the neural arch; this structure is similar to that described by Saint-Seine (1949) in *N. helenae*. In the anterior region the dorsal and ventral elements fuse to form ring centra, which also occur in *N. inimontis* and *N. denticulatus*.

(iii) Squamation. Contrary to Agassiz's (1844 : 294) opinion, the main body scales of *N. pentlandi* are rhomboid, although most of their hind edges are broken. In the young forms, however, the squamation is entirely cycloid (P1097); the scales are very similar to those of *Enchelyolepis* (Schultze 1966 : 276).

Notagogus parvus Traquair 1911

1911 *Notagogus parvus* Traquair : 26, pl. 4, fig. 10.

DIAGNOSIS. *Notagogus* attaining a standard length of 70 mm; mean proportions as percentage of standard length: head length 32%, trunk depth 32%; dorsal fin-ray counts: ant. 9, post. 11; scales cycloid.

HOLOTYPE. Specimen in the Musée Royale d'Histoire Naturelle, Bruxelles.

HORIZON AND LOCALITY. Wealden of Bernissart, Belgium.

MATERIAL. None examined.

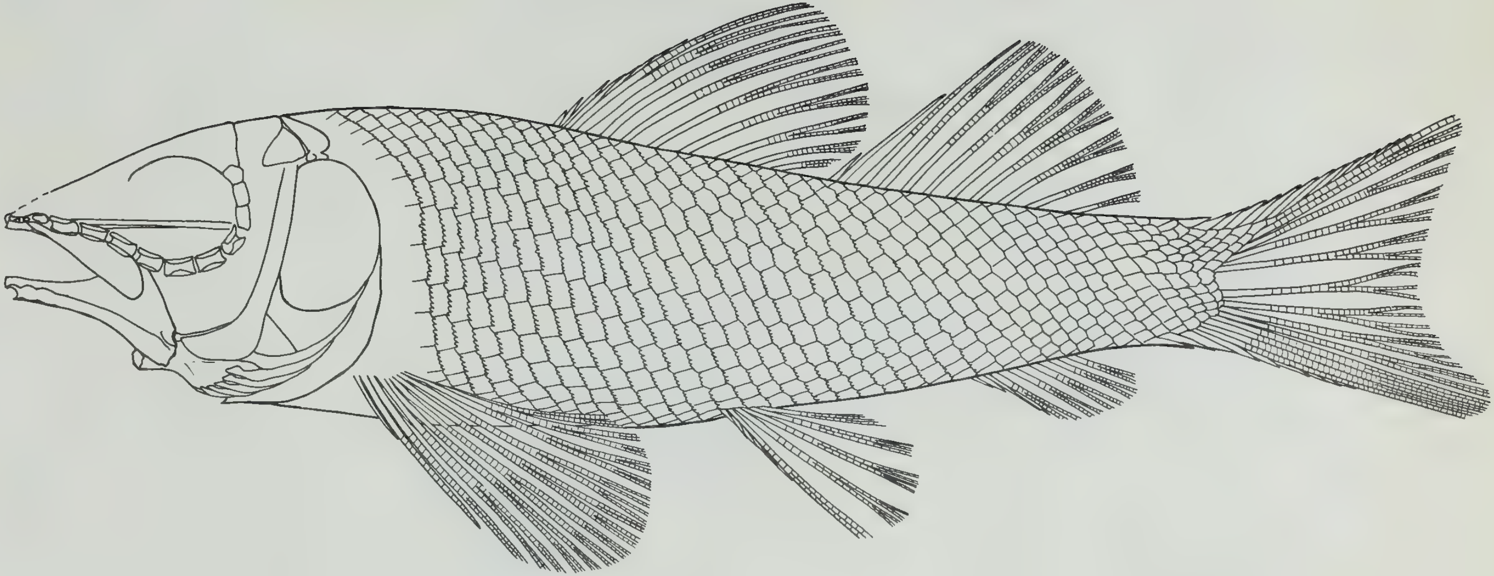

Fig. 43 *Notagogus decoratus* Eastman. Restoration of skeleton. × 2½ approx.

REMARKS. The material (eight specimens in the above Museum) is poorly preserved. The species is small (SL 70 mm) and is remarkable in possessing cycloid scales. As in *N. inimontis*, the vertebrae form complete rings.

Notagogus decoratus Eastman 1914

Fig. 43

1914a *Notagogus decoratus* Eastman : 360; pl. 7, fig. 3.

DIAGNOSIS. *Notagogus* attaining a standard length of 60 mm; mean proportions as percentage of standard length: head length 33%, trunk depth 22%, predorsal length 42%; dorsal fin-ray counts: ant. 9–10, post. 10–11; about 36 lateral line scales, only part of their hind borders bearing prominent serrations; no fringing fulcra on pectoral fin, a few on the dorsal and anal fins.

HOLOTYPE. Carnegie Museum, Pittsburgh, 5110.

HORIZON AND LOCALITY. Lower Kimmeridgian of Eichstätt region, Bavaria, Germany.

MATERIAL. CM 5110; specimen in Berger Museum, Blumberg near Eichstätt.

REMARKS. This species is reconstructed in Fig. 43. Although based upon a single small specimen, Eastman in describing this fish (1914a) was probably right to distinguish it from *N. denticulatus*, the other species of the genus occurring in Bavaria. It differs from *N. denticulatus* in its more elongated body, relatively larger pectoral fins and triangular dorsal fins.

Notagogus ferreri Wenz 1964

1964 *Notagogus ferreri* Wenz : 269, text-fig. 1; pl. 12b.

DIAGNOSIS. *Notagogus* reaching standard length of 30 mm; proportions as percentage of standard length: head length 30%, trunk depth 23%, predorsal length 39%; dorsal fin-ray counts: ant. 12, post. 11; 24 cylindrical vertebral centra; fringing fulcra present on caudal fin only.

HOLOTYPE. Specimen in the collection of L. Ferrer Condal.

HORIZON AND LOCALITY. Neocomian of Santa-Maria-de-Meya, Lerida, Spain.

MATERIAL. None examined.

REMARKS. This species is remarkable for its small size (total length 35 mm), although the single known specimen may be immature. Unlike other members of the genus, the centra are fully ossified rings throughout the column.

The trailing edge of the caudal fin is only slightly concave; it was supported by 10 rays, of which only six appear to form the lower lobe. This contrasts with the eight usual in macrosemiids. Young specimens of *N. pentlandi* also have fewer than eight lower rays so the low number in *N. ferreri* may again be due to immaturity.

DESCRIPTION. See Wenz (1964).

Family **UARBRYICHTHYIDAE** nov.

DIAGNOSIS. Medium to large, deep-bodied halecostome fishes; ganoine on postorbital region of skull roof forming radiating ridges; all sensory canals on skull of small diameter; frontoparietal suture slightly sinuous; nasals plate-like; supratemporal commissural sensory canal borne entirely by paired supratemporals which meet in the midline; fusion between infraorbital and supraorbital sensory canals behind the eye uncertain; sclerotic unossified; single supraorbital; six plate-like infraorbitals bearing ridges of ganoine; dermosphenotic probably fixed onto skull roof; no suborbitals; gape small, the jaw articulation lying below front of orbit; supramaxilla absent; dentary moderately curved, with sensory canal enclosed in tube; preopercular moderately curved, the sensory canal narrow and communicating with the exterior through narrow pores; distal ceratohyal deepening posteriorly only slightly; dorsal fin undivided, caudal fin forked, no epaxial fin-rays; scales rhomboid.

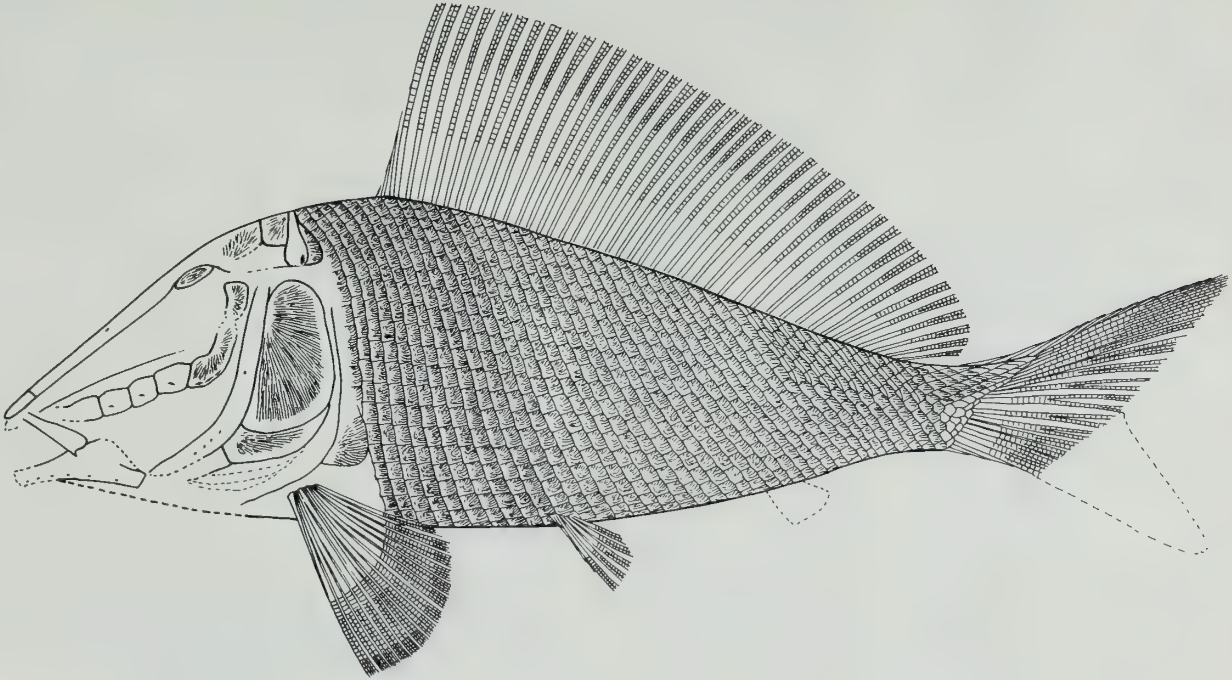

Fig. 44 *Uarbryichthys latus* Wade. Restoration of skeleton. × ½ approx.

RELATIONSHIPS. As explained below, this family is here excluded from the macrosemiids. However, *Uarbryichthys* does share with the macrosemiid *Macrosemius* one specialization unique among actinopterygians. Both genera have secondary transverse scale-rows above the main lateral line, although in *Uarbryichthys* these are confined to the caudal region. It must be presumed that this character arose in parallel in the two genera. On this evidence *Uarbryichthys* is here considered to be more closely related to the macrosemiids than to any other group, since it is not known to share unique specializations with any other holosteans. (The Cretaceous holostean *Aphanepygus* also has secondary transverse scale-rows (Bartram 1977), but these seem to be of a different type.)

Genus ***UARBRYICHTHYS*** Wade 1941

DIAGNOSIS. Uarbryichthyid reaching standard length of 260 mm; pectoral fin with about 15 rays, no fringing fulcra; dorsal fin with about 40 rays; caudal fin with 18 rays, fringing fulcra on dorsal edge only, long axial lobe covered by about six scale-rows; rhomboid scales ornamented with rugae of ganoine, hind edges smooth, secondary scale-rows intervening between transverse scale-rows above main lateral line in caudal region.

TYPE SPECIES. *Uarbryichthys latus* Wade 1941, the only species.

INTRODUCTION. The genus *Uarbryichthys* was erected by Wade (1941) to include a single species, *U. latus*, from the Jurassic fresh water deposits of New South Wales. Later Wade (1953) described this form more fully, together with another species from the same locality, *U. incertus*. He provides in his account no justification for this separation of species, and to judge from casts of the two specimens they are conspecific.

REMARKS. *Uarbryichthys* was placed within the Macrosemiidae by Wade (1953) on the basis of resemblances with *Ophiopsis* and especially *Histionotus*. But *Uarbryichthys* has neither of the two specializations which are unique to the macrosemiids, the nine infraorbitals and the interopercular remote from the mandible. It is thus excluded from the family here, and placed in a new family, the Uarbryichthyidae.

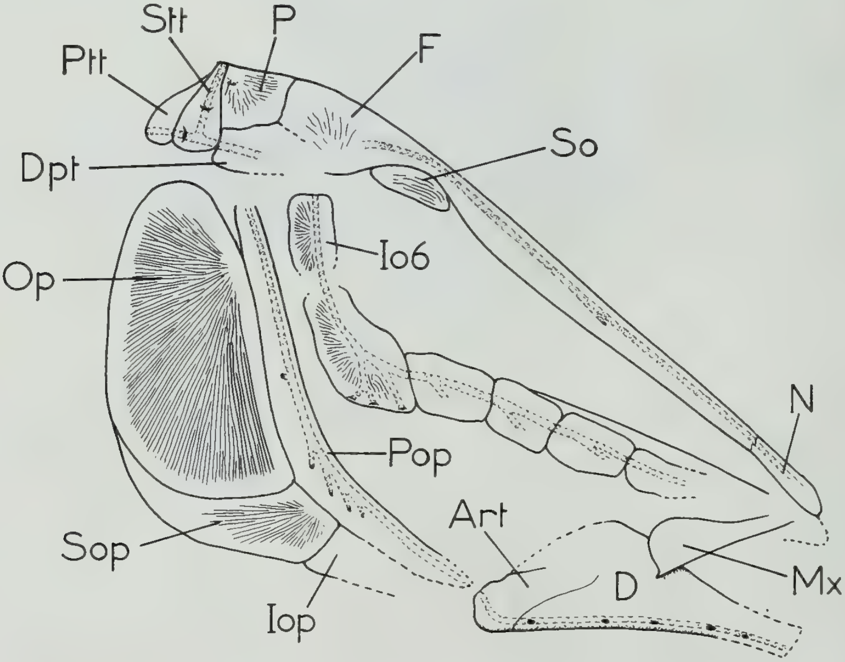

Fig. 45 *Uarbryichthys latus* Wade. Restoration of skull. × ½ approx.

Uarbryichthys latus Wade 1941

Figs 44, 45

1941 *Uarbryichthys latus* Wade : 82.
1953 *Uarbryichthys latus* Wade : 63, text-figs 1, 2; pl. 8.
1953 *Uarbryichthys incertus* Wade : 71; pl. 9.

Diagnosis. As for genus.

Holotype. Australian Museum, Sydney, F43258a, b.

Horizon and Locality. Jurassic of Talbragar, New South Wales, Australia.

Material. AM: F43258a, b, F43606.

Remarks. The two known specimens of *Uarbryichthys* are preserved in impression in fine-grained chert. These enabled Wade to give a fairly complete description of the squamation, fins and of the dermal bones of the head. The specimens have been re-examined by means of rubber casts, now in the British Museum (Natural History), and Wade's description checked; it seems to be as good as the preservation of the material will allow.

Infraclass **CHONDROSTEI**

Order ***incertae sedis***

Genus ***TANAOCROSSUS*** Schaeffer 1967

? ***Tanaocrossus maeseni*** (Saint-Seine 1962)

1962 *Macrosemius maeseni* Saint-Seine in Saint-Seine & Casier : 8; pl. 2, figs 1, 2.

Diagnosis. ? *Tanaocrossus* with dorsal part of body above notochord devoid of scales.

Holotype. Musée Royale de l'Afrique Centrale, Tervuren, 8304.

Horizon and Locality. Kimmeridgian of Songa, Zaïre.

Remarks. Saint-Seine's description of this fish is based upon a single, poorly preserved specimen. He placed it in the genus *Macrosemius* on account of the elongated dorsal fin, which extends from the skull to the caudal fin, and of the large area on either side of the dorsal fin devoid of scales. The bones of the skull, however, are crushed beyond confident recognition and Saint-Seine (in Saint-Seine & Casier 1962 : 9) states that his reconstruction of the head is 'en grande partie hypothétique'.

The first character which suggests relationship to *Macrosemius*, the long dorsal fin, is found in diverse actinopterygian groups and is of little use as an indicator of relationship, as discussed below. The dorsal scale-free area, however, is found elsewhere only in *Macrosemius* and *Legnonotus*, and is stronger evidence of relationship.

There are other features of Saint-Seine's fish which render this relationship unlikely, however. For instance between successive neural spines are two or three short slender bones. Saint-Seine identified these as axonosts (proximal dorsal fin radials), and the rods beneath the dorsal fin-rays as baseosts (middle segments of the radials). This identification is probably correct, as the two elements correspond closely in number; the lower series cannot consist of supraneurals since these occur well in excess of the number of neural spines. The possession of elongate baseosts appears to be a primitive feature which occurs in chondrosteans (*Pteronisculus*, *Birgeria*, *Tarassius*, *Bobasatrania*). In contrast the baseosts of *Macrosemius* and other Neopterygii are short and stout. Also in contrast to *Macrosemius*, Saint-Seine's specimen displays non-branching fin-rays, an unusual feature which rarely occurs in fish other than chondrosteans.

One holostean feature is present, however. The dorsal fin-rays show a one-to-one relationship with their radials. But this feature is also found in the chondrostean Haplolepidae and Perleididae.

Of the known Chondrostei, *Tanaocrossus kalliokoskii* Schaeffer (1967 : 316; pl. 20) from the Upper Trias of Colorado resembles Saint-Seine's fish most closely. They share a similar number (about 75) of non-bifurcating dorsal rays and of caudal fin-rays (about 15). The shape of the body and of the known fins are also very similar. Only the rear part of the skull is known in *T.*

kalliokoskii; the form of the opercular and of the plate-like preopercular bones are taken by Schaeffer (1967 : 316) to indicate chondrostean affinities. The squamation of this species is, however, entire.

Although the similarities between *M. maeseni* and *T. kalliokoskii* are few, the features they share in fin form and ray number are rare among the chondrosteans, to which both fishes seem to belong. For this reason, *Macrosemius maeseni* is here provisionally transferred to *Tanaocrossus*. A brief and inconclusive discussion of the relationships of *Tanaocrossus* is given by Schaeffer (1967 : 317).

The Macrosemiidae in comparison with other Actinopterygians

It will be argued in the succeeding section that the seven genera described above constitute a monophyletic group. In this section their structure is reviewed and compared with that of other actinopterygians. The features which they share with other groups are assessed in the light of the partially cladistic classification of Patterson (1973), in preparation for the discussion of the relationships of the macrosemiids.

(i) Skull roof and braincase. In all macrosemiids (but not in *Uarbryichthys*) the supratemporal commissural sensory canal is enclosed in part by the parietal (possibly a compound parieto-supratemporal, as discussed on p. 143). Many teleosts (e.g. Notopteridae, Osteoglossoidei, Characidae, Gymnotidae) also display this condition (McDowell 1973 : 12).

The sensory canals on the skulls of macrosemiids are remarkable for their large diameters. In groups below the teleost level the canals are housed in tubes of narrow bore and communicate with the surface through fine pores; in most macrosemiids the canals are exposed by large fenestrae. This character was presumably derived independently within the family, since the sensory canals on the skull roof of *Notagogus*, and on the entire skull of *Uarbryichthys*, are enclosed in narrow tubes. The functional significance of large sensory canals in the macrosemiids is unclear; they presumably conferred a high sensitivity on the enclosed sensory organ (Marshall 1971 : 55). Such wide canals are found among teleosts in bathypelagic forms (macrourids, halosaurs).

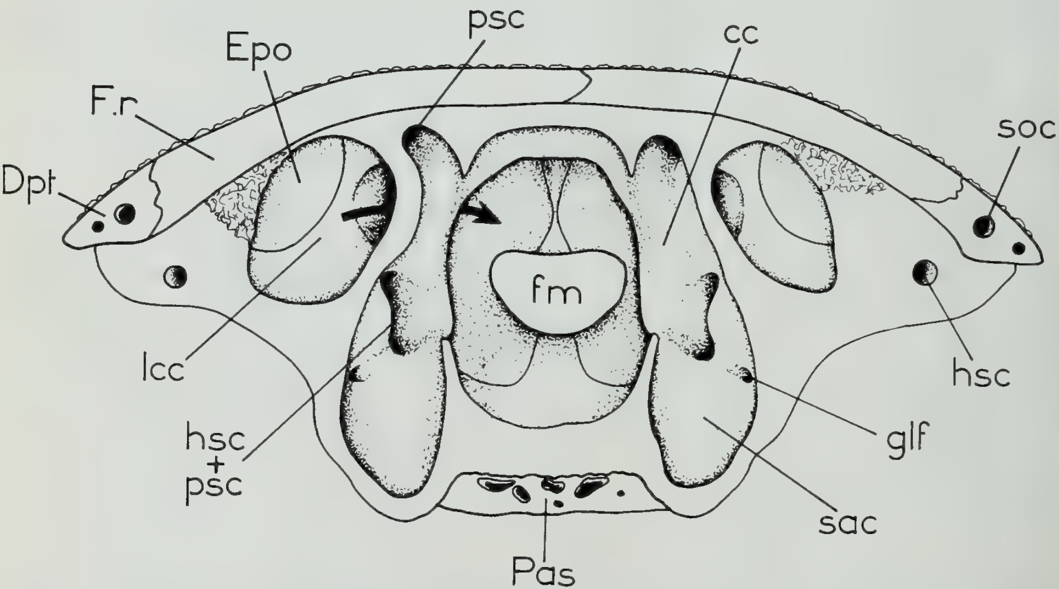

Fig. 46 *Lepisosteus osseus* (Linnaeus). Skull roof and braincase cut transversely through the otic region and viewed from in front to show the lateral cranial canal (arrowed). × 3.

Unfortunately the macrosemiid braincase is known only in medial view in a single specimen of *M. rostratus* (Fig. 3, p. 144). Apart from the occipital fissure, the postorbital chondrocranial ossifications of palaeoniscids fuse together in the adult and give no indication of the primitive actinopterygian ossification pattern. Among neopterygians the occipital fissure occurs only in parasemionotids, pholidophorids (Patterson 1975) and pachycormids (Lehman 1949). In other groups the fissure is obliterated, sometimes by the expansion of the surrounding bones. This has occurred in *Macrosemius*, in which the exoccipital has grown forward and enclosed the vagal canal, as in *Lepidotes* (Rayner 1948). According to Patterson, closure of the fissure has occurred independently in several groups, making this specialization a weak indicator of relationships.

Several braincase bones exhibit a variable occurrence among neopterygians; these are the opisthotic, pterotic, intercalar and supraoccipital. Patterson considers that the first three, and possibly also the last, occurred primitively in actinopterygians. The opisthotic is missing in *Macrosemius*, in which the exoccipital and prootic meet. Among teleosts the opisthotic is absent in all living groups and some pholidophorids, and in halecomorphs it is known to be lost in *Amia* and one species of *Caturus* (*C. furcatus*, Patterson 1975 : 441). It is also lost in *Lepisosteus* and *Lepidotes* (Patterson 1975). The pterotic is present in *Macrosemius* immediately beneath the skull roof, the primitive position of the bone, according to Patterson, as found in caturids, parasemionotids, *Pachycormus*, and probably also *Dapedium*. Again according to Patterson, the intercalar was primitively an endochondral ossification, as retained in parasemionotids and *Pachycormus*. This bone is lost in *Lepisosteus* and *Lepidotes*. A membranous component of the intercalar evolved independently in halecomorphs and teleosts; in *Amia* and living teleosts the endochondral part is lost. In the specimen of *Macrosemius* mentioned above, the inner view of the skull reveals no endochondral intercalar, and of course the membranous component would not be visible in this view even if present. There exists one specimen (Mü AS.1.770) which would probably indicate whether a membranous intercalar is present or not, but it was not available for development in acetic acid. Finally, the supraoccipital is certainly present only in pholidophorids and teleosts (Patterson 1975). It is unknown in *Macrosemius*.

The basisphenoid is not preserved in the specimen of *Macrosemius* displaying the braincase, and may have been absent; as described above, its position is partly occupied by a short, stout pedicel arising from the parasphenoid which divides the entry of the myodome into two. As mentioned above, a similar though smaller process has been found in a palaeoniscid (*Kansasia*) and in pholidophorids and leptolepids. A feature unique to the teleosts, the extension of the posterior myodome beneath the basioccipital, does not occur in macrosemiids as far as is known.

What little is known of the macrosemiid braincase, therefore, gives no evidence of relationship with either the halecomorphs or teleosts.

(ii) Circumorbital series. With the exception of the dermosphenotic, the infraorbital series of *Macrosemius*, *Histionotus* and *Propterus* (the only macrosemiid genera in which the series is known) is remarkably uniform in shape and number. All possess a long tapering antorbital, seven scroll-like infraorbitals below the eye and two tubular infraorbitals behind the eye. There are no suborbitals.

In *Macrosemius*, *Histionotus* and *Propterus* the dermosphenotic forms a short, vertical, perforated tube around the upper part of the infraorbital sensory canal; it resembles the last two infraorbitals, although it appears to have been attached to the skull roof. As in most recent teleosts (Gosline 1965 : 188) the bone does not enclose the junction between the infraorbital and supraorbital sensory canals. In *Notagogus*, in contrast, the dermosphenotic encloses this junction and is fully incorporated into the skull roof. The relationship of the dermosphenotic to the skull roof in various groups has been discussed by Patterson (1973 : 244). In palaeoniscids, pycnodonts and halecomorphs the dermosphenotic is fully incorporated into the skull roof. Elsewhere, the bone is either hinged to the roof, as in *Lepisosteus*, or overlies the sphenotic forming a loose attachment, as in teleosts. Patterson suggests that the former pattern may be primitive, and that the infraorbital-like dermosphenotic of *Lepisosteus* and teleosts is specialized. If this is the case then *Notagogus* displays the primitive macrosemiid condition. In fact the difference between the two types of dermosphenotic may not be profound. The state of the bone is known to change during the development of *Amia*. It originates as a vertical tube around the upper part of the sensory canal, and closely resembles the infraorbitals (Pehrson 1940). Later in ontogeny the bone develops membranous outgrowths and becomes part of the skull roof. If this mode of development was widespread among actinopterygians then the acquisition of an infraorbital-like dermosphenotic within the Macrosemiidae and other groups may have involved a relatively simple process of growth retardation.

The infraorbitals of macrosemiids resemble those of many teleosts. It is generally accepted that the canal-bearing bones of fishes involve two components (Kapoor 1970 : 86). The laterosensory component forms a tube around the sensory canal, from which the laminar component extends. In teleosts the membranous laminar component develops first, and the laterosensory component forms later in association with an invaginating neuromast organ. The two components may be fused from the beginning (*Phoxinus*, *Alburnus*), or may fuse later (*Leuciscus*, *Ophicephalus*) or may remain separate (*Nemacheilus*). In some cases the laterosensory component alone develops. Thus of the five infraorbitals present in mormyrids (Taverne 1971), for example, the posterior three form tubes around the sensory canal; the other two are scroll-like, incompletely surrounding the canal. A similar process seems to have occurred in the Macrosemiidae, in which the antorbital and last two infraorbitals consist of the laterosensory component only. The remaining infraorbitals, forming open gutters around the sensory canal, may comprise a small membranous component in addition.

Patterson (1973) notes that the suborbitals are lost within the Amiidae and within the pholidophorid–teleost group. Although this loss occurred independently within the two groups, he suggests that it may nevertheless indicate relationship between them since this feature is rare elsewhere. It is also found in the Pycnodontidae (Lehman 1966 : 177, *Macromesodon*) and in the chondrostean *Errolichthys* (Nielsen 1955), as well as in the macrosemiids.

It seems that many features of the macrosemiid skull (the scroll-like nasals and infraorbitals, the trough-like preorbital region of the frontals, the absence of suborbitals and the form of the dermosphenotic) are manifestations of a trend involving the general reduction of laminar dermal bone. These features are emphasized by the large size of the sensory canals. In *Uarbryichthys* none of the bones form troughs or scrolls; the sensory canals are housed in narrow tubes. Suborbitals are absent in this genus too, however.

(iii) Hyopalatine bones. The ossifications in the palate of macrosemiids conform to the usual neopterygian pattern, such as that of *Amia*. The presence of two dermopalatines (known in *Macrosemius*) is probably a primitive feature as Patterson (1973 : 246) suggests; it is found in the chondrosteans *Pteronisculus* (Nielsen 1942), *Elonichthys* (Watson 1925) and in some individuals

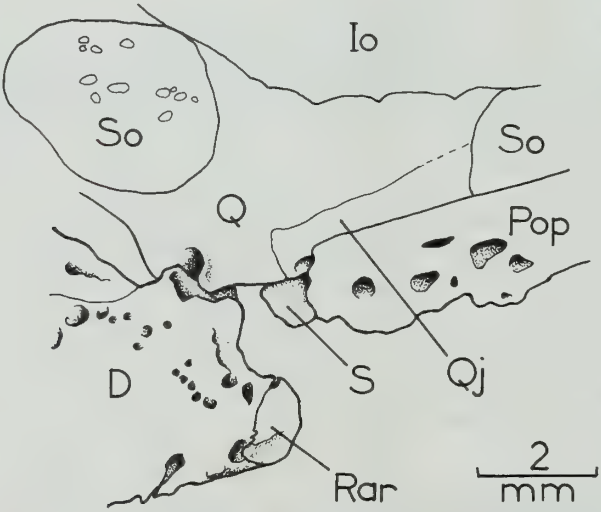

Fig. 47 *Furo longiserratus* (Agassiz). Region of left jaw articulation of CM 5021.

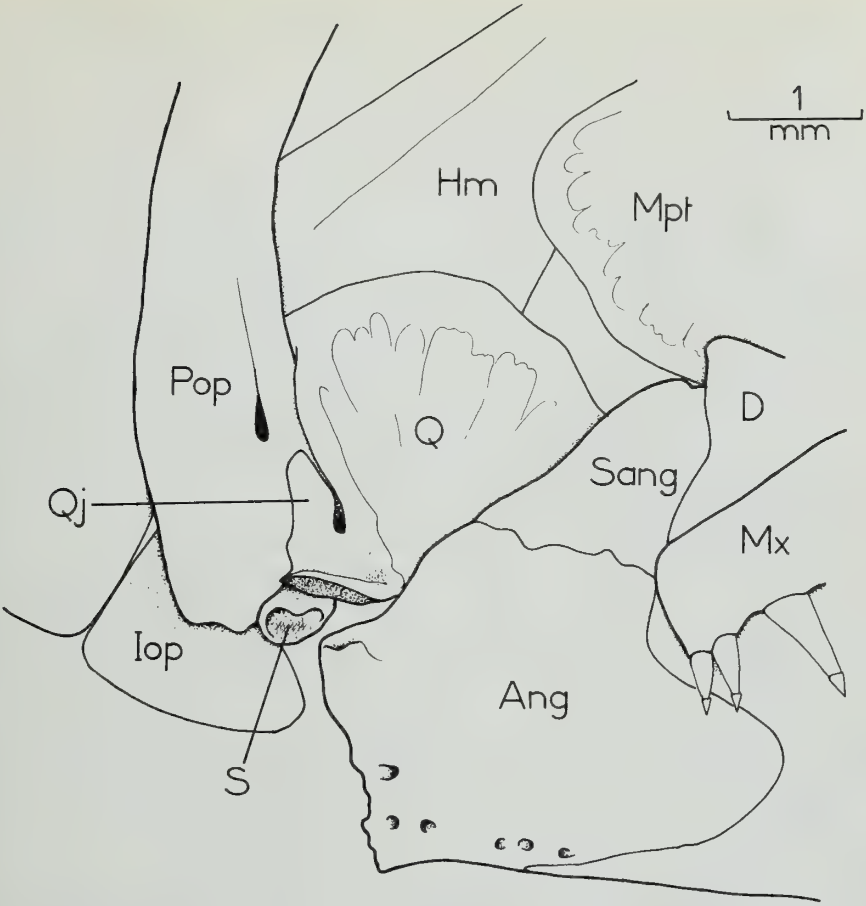

Fig. 48 *Caturus* sp. from the Lower Kimmeridgian of Bavaria, P44900. Region of right jaw articulation.

of *Ospia* (Stensiö 1932 : 252), as well as in *Amia*. The palate of macrosemiids usually ossifies fully, although a gap may persist between the metapterygoid and quadrate.

The neopterygian quadrate is associated with a separate ossification of the hyomandibular cartilage, the symplectic, and with a dermal bone, the quadratojugal. Patterson (1973) has discussed at length the relationships between these three elements.

Three patterns may be recognized. In *Lepisosteus*, *Lepidotes* and *Dapedium* (Patterson 1973 : figs 6, 26) the quadratojugal is an elongated bone lying along the upper edge of the ventral arm of the preopercular; the anterior end of the bone abuts against the articular condyle of the quadrate. No fusion occurs between the quadratojugal and quadrate in *Lepisosteus* and in Patterson's specimens of *Lepidotes* and *Dapedium*. In none of these forms does the symplectic come into contact with the mandible. In *Lepisosteus* the symplectic is small and remote from the quadrate; in *Lepidotes* and *Semionotus* it forms a long rod lying medial to the quadrate and quadratojugal.

The second pattern is found in living teleosts and their fossil relatives. The quadratojugal is probably represented by the spine-like posterior process of the quadrate, as held by Holmgren & Stensiö (1936 : 463). This condition is advanced relative to that of *Lepisosteus*, in which the quadratojugal remains discrete. The symplectic of teleosts is typically a long tapering bone which is inserted into a groove formed between the quadrate and its posterior process on their inner surface; thus in these fish too no contact between the symplectic and the lower jaw occurs.

The third group comprises the Parasemionotidae, Caturidae and *Amia*. In these forms the quadratojugal is absent (*Amia*) or reduced to a small flange of bone on the quadrate as in parasemionotids (Patterson 1973 : fig. 23), *Furo* (fig. 20) and *Caturus* (Fig. 48). Patterson suggests that this reduction of the quadratojugal is a derived character; it probably is, but it must have been acquired several times in these groups, since a large, discrete quadratojugal is present in *Furo longiserratus* (Fig. 47), in specimens CM 5021a and BM(NH) 37081. The symplectic of *Amia* is unique among living holosteans and teleosts in forming an articulation with the lower jaw, posterior to that of the quadrate (Allis 1897: pl. 20). Such an articulation also occurs in the parasemionotids and caturids (Patterson 1973 : figs 20, 23). With some hesitancy Patterson holds that the symplectic jaw articulation is a major specialization acquired independently by these fishes, indicating that they form a monophyletic group, the Halecomorphi.

The quadratojugal in the Macrosemiidae is a long stout bone lying along the entire length of the ventral arm of the preopercular. The expanded anterior end of the bone fits tightly behind the thin lateral part of the large articulatory condyle of the quadrate. In *Macrosemius* and perhaps also in *Histionotus* and *Notagogus*, fusion occurs between these two bones in this region; the quadratojugal of *Propterus* remains free. In teleosts the quadrate and quadratojugal are fused from the beginning or fuse early in ontogeny, and Patterson considers this to be a teleost specialization. In macrosemiids, in contrast, if fusion occurs at all, the two bones fuse late in development. This is probably also true of the 'semionotids' (Patterson, pers. comm.).

The macrosemiid symplectic is known only from one specimen of *Propterus elongatus*, although the identification of this bone is not certain, as discussed on pp. 172–3. Whatever the form of the symplectic in this family, there is no evidence to suggest that it formed an articulation with the lower jaw. Only one articulatory facet occurs on the mandible, and this is fully occupied by the broad quadrate condyle. For this reason it is unlikely, in the present state of knowledge, that the Macrosemiidae are halecomorphs.

The hyomandibular of *Macrosemius*, *Propterus* and *Histionotus* displays a specialization in the form of a long flange on the outer surface, alongside the leading edge of the preopercular. Osse (1969 : 383, fig. 24a) has discussed the function of a similar flange in *Perca*, in which it serves for the origin of the upper part of the adductor mandibulae muscle. This narrow zone of origin for the muscle leaves the lateral surface of the hyomandibular anterior to the flange free for the insertion of the long levator arcus palatini muscle. The latter is unusually long, its length presumably compensating for the restricted area available for its origin on the short postorbital region of the skull. Since the postorbital region is also short in the macrosemiids, the flange on the hyomandibular may have arisen to meet similar functional demands, that is, to allow for the presence of an elongated levator arcus palatini muscle.

(iv) Dermal upper jaw. The supramaxilla is lacking in the Macrosemiidae; the absence of this bone is very rare among fish with a free, mobile maxilla. It is absent in the pycnodonts, *Besania*, *Luganoia* (Brough 1939 : figs 15, 20) and in *Acentrophorus* (Gill 1923). There is a single supramaxilla in the remaining 'semionotids' and in the Halecomorphi, and two in the pholidophorids and primitive living teleosts. In *Elops* (Vrba 1968 : 228, fig. 3), the posterior ends of the supramaxillae are fixed to the maxilla; when the jaws open, 'the supramaxillae fold out as from a fan, providing some firmness to the unprotected lateral wall of the mouth'. This function was presumably primitive for holosteans and teleosts, since there seems to be no other explanation to account for the evolution of the supramaxilla in these fishes. In *Amia calva*, however, the supramaxilla is firmly fixed to the maxilla and clearly in certain other groups, for example the pachycormids (Wenz 1968 : figs 52, 67), the bone was also incapable of performing the function described in *Elops*.

The absence of the supramaxilla in the forms listed above is associated with the possession of short jaws, where the area of the walls of the open mouth is small and thus may have needed less support than in long-jawed forms. In *Macrosemius* and *Propterus* such support may have been provided by the ventral extensions of the anterior three infraorbitals. There are no means of knowing, on present evidence, whether the absence of the bone in macrosemiids is a primitive halecostome feature, or whether it is due to secondary loss. The bone is also absent in *Uarbryichthys*.

The number and form of the maxillary teeth in the macrosemiids varies. A long row of maxillary teeth occurs in *Legnonotus* and *Notagogus*; these genera probably took small prey. In *Macrosemius* and *Propterus* the maxillary teeth are reduced in size and number, and restricted to the posterior part of the maxilla; in *Histionotus* they are absent. In *Macrosemius* at least, the vomers, palatines and splenials bear a crushing dentition. The coincidence of a reduction or absence of maxillary teeth and the possession of a crushing dentition occurs in the pycnodonts and in some 'semionotids', for example *Dapedium politum* (Wenz 1968) and *Acentrophorus varians* (Gardiner 1960).

The macrosemiid premaxilla forms a stout 'ascending process', renamed the nasal process by Patterson (1973). The process passes beneath the nasal and forms a suture with the dorsal ethmoid ossification. The nasal process is known also in *Lepisosteus*, *Amia*, caturids, 'semionotids', parasemionotids and *Perleidus* (Patterson 1975), and appears to be a primitive feature of the Neopterygii. The nasal process of *Amia* develops as a separate ossification, the rhinal bone of Bjerring (1972 : 193), and Patterson (1975 : 512) has shown that in teleosts and their fossil relatives the process separates from the dentigerous part of the premaxilla, forming 'dermethmoids'. In living teleosts these may fuse with the rostral or become incorporated into the mesethmoid.

The nasal process of *Lepisosteus*, *Amia*, *Lepidotes* and *Semionotus* completely surrounds the olfactory nerve and lines the nasal pit. In macrosemiids, however, the process passed lateral to the nerve and did not enclose it. A similar relationship between the olfactory nerve and nasal process occurs in *Ophiopsis* (Bartram 1975), *Furo latimanus* (personal observation), *Dapedium*, *Acentrophorus*, parasemionotids (Patterson, 1975: figs 134, 136, 137), and possibly also in *Luganoia* (Brough 1939: 46).

(v) Lower jaw. Macrosemiids possess the following dermal elements in the mandible, in common with *Amia*, *Lepisosteus* and *Pholidophorus* (Patterson 1973 : fig. 7): dentary, angular, surangular, prearticular and coronoids (one in *Macrosemius*).

The Meckelian cartilage in macrosemiids forms two ossifications. The larger forms the broad, rearward-facing facet for the quadrate, and the tall coronoid process. The second ossification is the retroarticular. Among living forms this bone occurs in *Lepisosteus*, *Amia* (ossicle 'a' of Bridge, Allis 1897 : pl. 20) and in the teleosts (angular of Goodrich (1930), Gosline (1969)). Nelson (1973 : 179) has considered the relationship between the retroarticular and the facet for the jaw articulation. Referring to extant forms he notes that in *Latimeria*, *Lepisosteus*, *Amia* and in some osteoglossomorph (*Arapaima*, *Heterotis*) and elopomorph teleosts, the retroarticular forms part of this facet. He considers this to be the primitive condition; in most teleosts the retroarticular is excluded from the joint. However, the retroarticular also appears to be excluded from the joint in some non-teleost fossils (*Macrosemius*).

(vi) Preopercular, hyoid arch and opercular series. These elements display several features of special interest in the macrosemiids: the small size of the interopercular, the form of the branchiostegal rays and the absence of a gular.

The upper branchiostegal rays of macrosemiids are acinaciform; that is to say they form curved, overlapping, non-laminar blades. Acinaciform branchiostegals, of a different type, have previously been known only in the higher teleosts (McAllister 1968 : table 1). The branchiostegal rays of most chondrosteans and holosteans are spathiform, forming laminar, scarcely overlapping plates, as in the palaeoniscids (Nielsen 1942), parasemionotids (Lehman 1952), pachycormids (Lehman 1949), *Amia* (Jessen 1968) and *Caturus* (Fig. 50). The hyohyoideus muscle in these fossil groups presumably formed a continuous sheet over the inner side of the branchiostegal rays, as in *Amia*, *Salmo*, *Clupea*, *Albula* and *Esox* (Edgeworth 1935 : 101). This muscle probably performed the function ascribed to it by Vrba (1968 : 227) in *Elops*, in which it contracts during inspiration, holding the branchiostegal membrane against the sternohyoideus musculature and preventing the inflow of water into the opercular cavity. This is undoubtedly the primitive function of the muscle.

In higher teleosts, however, an active branchiostegal pump occurs which supplements the action of the operculum in lowering the pressure in the opercular cavity (Baglioni 1907). In such fish, the branchiostegal rays are highly movable, and are spread and collapsed like a fan by the action of the modified hyohyoideus muscle. Thus in *Perca* (Osse 1969 : 335, fig. 12), the hyohyoideus muscle differentiates into a superior portion which passes from ray to ray, and an inferior part which connects each ray to the ceratohyal. Contraction of the hyohyoideus inferior thus expands the branchiostegal membrane, and the contraction of the hyohyoideus superior collapses the membrane. The form and overlapping of the branchiostegals in macrosemiids suggest that members of this family also possessed a branchiostegal pump mechanism. That this was the case is supported by the fact that most macrosemiid specimens are preserved with the branchiostegal rays widely spread, presumably by the action of a hyohyoideus inferior muscle.

The mandible in chondrosteans was presumably depressed by the action of muscles connecting it with the hyoid arch (Millard 1966 : 37). In holosteans and teleosts, however, another mechanism has arisen involving a new element, the interopercular. With the exception of the pycnodonts, the interopercular is present in all actinopterygians in which the maxilla is movable. Patterson (1973 : 246) can find no evidence to suggest that its absence in *Lepisosteus* is due to loss, and considers this absence to be a primitive feature shared with the Chondrostei.

In *Amia* (Allis 1897 : pl. 20) ligaments extend from the retroarticular in the mandible to the interopercular, to the uppermost branchiostegal ray and to the proximal ceratohyal, and from the latter bone to the interopercular. A similar set of couplings occurs in living teleosts (*Elops*, *Albula*, *Clupea*, *Salmo* – Gosline 1969 : 192). The lowering of the mandible by the pull of these ligaments may be brought about in various ways. Thus contraction of the levator operculi muscle would cause backward movement of the interopercular and of the ceratohyal, to which it is connected, or a similar movement of these two bones may be caused by contraction of the sternohyoideus muscle.

In *Lepisosteus*, in which the interopercular is absent, a long, thick ligament extends from the retroarticular to the proximal ceratohyal (personal observation; this contradicts Gregory's (1933 : 127) observation that this ligament ran to the quadratojugal, which he called the interopercular). If Patterson is correct in considering the absence of an interopercular in this fish a primitive feature, and *Lepisosteus* the most primitive known neopterygian, then the presence of a hyoideomandibular ligament and an indirect method of opening the jaws in this fish is surprising, since it suggests that they arose before the appearance of the interopercular. The view that this ligament is the more primitive is held by Gosline (1969 : 192), who points out it is very large in *Amia*, in which the interopercular has little to do with the opening of the mouth. Following her work on *Elops*, Vrba (1968 : 232) arrives at the same conclusion.

But the fossil evidence, in contrast, seems to indicate that the interopercular was involved in the opening of the mouth from an early stage in the evolution of the halecostomes, and indeed arose in association with this function. Thus in fossil forms in which the jaw articulation has shifted forward (*Lepidotes*, *Semionotus*, *Dapedium*, *Pholidophorus*, *Lycoptera*) the interopercular is very long and maintains a close proximity to the hind end of the mandible. This correlation also occurs in teleosts with forwardly-placed jaws, for example *Chanos* and the cyprinoids. In the perch (Osse 1969 : 337, 359) the mandible is depressed by the contraction of the levator operculi muscle acting *via* the interoperculomandibular ligament.

In view of these facts, the remoteness of the interopercular from the mandible in macrosemiids is surprising. The significance of this feature is not clear; whichever tendons inserted upon the retroarticular must have been very long. There is some evidence to indicate that the uppermost branchiostegal ray was modified, serving for the origin of a tendon which inserted upon the lower jaw, as in *Amia*. The proximal ends of the lowermost seven rays are expanded and articulated with the lateral surface of the ceratohyal; in contrast, the uppermost ray tapers proximally forming no such expansion, and its blade was overlapped by, and probably fixed to, the subopercular.

The gular plate has been lost in most living actinopterygians. The median gular is retained in *Amia*, Elopidae, Megalopidae, *Albula* (Nybelin 1960) and *Luciocephalus* (Liem 1967 : 118). Among fossil holosteans the gular is known to be lost only in *Lepidotes*, pycnodonts, aspidorhynchids and macrosemiids. In all living forms with a gular, this bone is connected to the mandibular rami by a division of the intermandibular muscle. and to the ceratohyals by the interhyoideus muscles (Liem 1967 : 118). During respiration and feeding, the anterior ends of the ceratohyals are pulled downwards by the action of the sternohyoideus muscles, depressing the gular and hence the floor of the mouth. Thus the gular serves to spread over a large area of the floor of the mouth what would otherwise be a local effect. The loss of the gular in the Macrosemiidae and in most teleosts may be associated with the forward position of the jaw articulation. Gosline (1967 : 238) has noted the correlation between the latter feature and the presence of a short ceratohyal. Such a ceratohyal, with its anterior end at the level of the quadrate condyle as in macrosemiids, is in no position to depress a gular plate, unless this were very large; this may partly account for the loss of the bone.

(vii) Vertebral column. Monospondylic ring centra are present in the abdominal region of *Macrosemius*, *Histionotus* and *Enchelyolepis*. These centra are thick, constrict the notochord and fuse with the arches; their greater part was composed of perichordal, endochondral bone. Although the anterior vertebrae of *Notagogus* also form rings, these separate into dorsal and ventral crescents in the caudal region. Whether they are mainly chordacentral or not is difficult to assess. In *Propterus elongatus*, centra are formed only in the first few segments; they consist of dorsal crescents alone, and are probably chordacentral.

The Neopterygii present a rich diversity of central ossification patterns in both origin (chorda- or autocentral) and form (rings, solid cylinders or crescents). Thus thin ring-like chordacentra are present in the teleosts *Ichthyokentema* (Griffith & Patterson 1963 : 26, fig. 12), *Catervariolus* (Saint-Seine 1955 : fig. 47) and *Euthynotus* (Wenz 1968); such centra have not been recorded in halecomorphs. Thick centra, composed mainly of endochondral bone and constricting the notochord like those of *Macrosemius*, are found in the Caturidae. They may form crescents, as in some species of *Furo*, *Caturus* and *Osteorachis* (Patterson 1973 : 281) or thick annuli, as *F. microlepidotus*, *Neorhombolepis* (Woodward 1918 : 87), *Macrepistius* (Schaeffer 1960 : fig. 5) and *Ophiopsis* (Bartram 1975). In the last genus, the presence of dorsal and ventral hemichordacentral components has been demonstrated, and such a chordal contribution to annular centrum formation probably occurred in other caturids.

The neural spines of macrosemiids are known in the abdominal and caudal regions in *Propterus* and *Enchelyolepis*; they are paired. Paired neural spines occur also in chondrosteans and *Lepisosteus*, and this is probably the primitive neopterygian condition (Patterson 1973 : 236). Median neural spines are found in the caudal regions of *Amia* and the teleosts, and Patterson considers

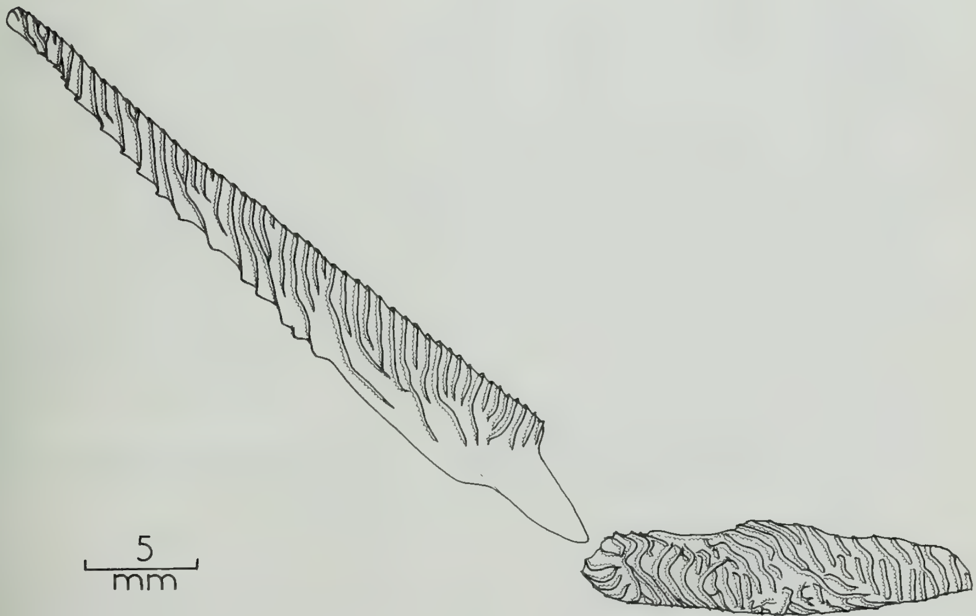

Fig. 49 *Amia calva* Linnaeus. Serrated appendage and denticle-bearing plate of right side.

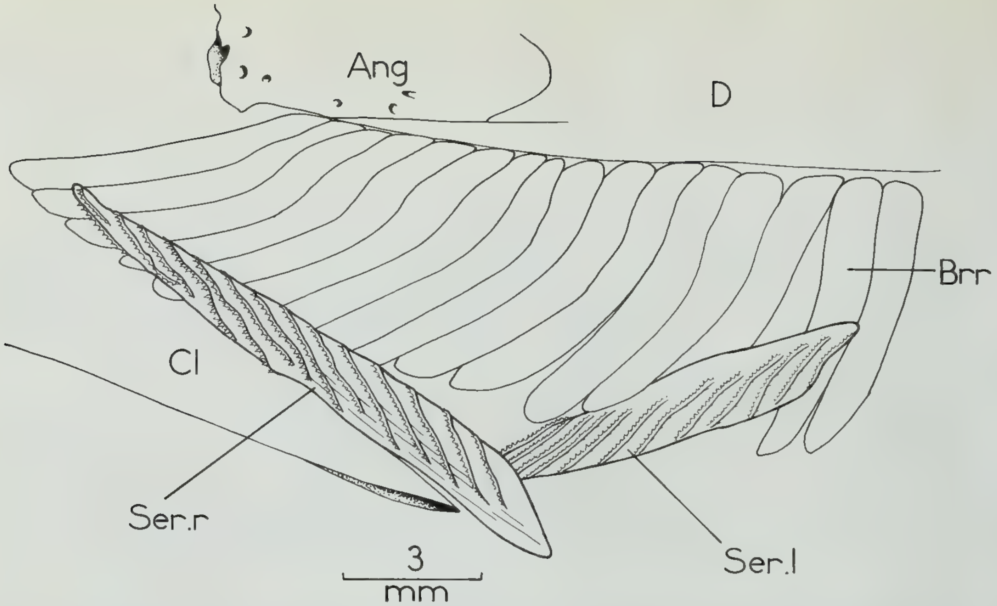

Fig. 50 *Caturus* sp. from the Lower Kimmeridgian of Bavaria, P44900. Left and right serrated appendages, branchiostegals and ventral parts of mandible and cleithrum, as preserved.

this specialization indicative of relationship between these two groups; it also occurs in their fossil relatives. Median neural spines also occur in *Dapedium*, *Tetragonolepis* and pycnodonts (Patterson 1973) and in the palaeoniscoids *Australosomus* and *Birgeria* (Nielsen 1949). The presence of paired neural spines in the Macrosemiidae provides a strong indication that this family belongs neither in the Halecomorphi nor in the Teleostei.

(viii) Pectoral girdle and fin. The discovery of a serrated appendage in one specimen of *Propterus elongatus* is of special interest, since such a bone is known to occur only in *Amia* (Fig. 49; Wilder 1876 : 259) and *Caturus* (Fig. 50). That of *Amia* is discussed by Liem & Woods (1973).

Both left and right serrated appendages are preserved in an acid-prepared specimen (BM(NH) P44900) of *Caturus* ?*furcatus* of standard length 130 mm. The right appendage, the better preserved, lies along the ventral arm of the cleithrum. Its surface is traversed by 14 ridges bearing small, three-spined denticles pointing posteriorly; similar denticles occur in vertical rows on the cleithrum. As in *Amia*, the ridges slope forward dorsoventrally, although in contrast to *Amia*, the ridges are all of approximately equal length and do not branch. The proximal end of the appendage was presumably embedded in the sternohyoideus musculature, the remainder of the bone projecting freely into the opercular cavity. That the appendage did project, rather than lie embedded in the skin, is indicated by the presence of denticles on the medial surface; these are visible in the specimen at the distal tip of the bone. In addition to the appendage, *Amia* also possesses a flat plate of bone, also bearing denticulated ridges, embedded in the skin covering the sternohyoideus muscle; this is absent in the specimen of *Caturus*.

The serrated appendage of *Propterus* differs from those described above in forming only a single row of denticles along the leading edge. Its curved form suggests that it did indeed project into the opercular cavity.

The homologies of these denticle-bearing plates and appendages are not obvious. The most likely candidate is the clavicle of chondrosteans and crossopterygians (Liem & Woods 1973). In the former, the ventral arm of the cleithrum is very short and preceded by a large clavicle, as in *Acipenser* (Jessen 1972 : fig. 2). The sternohyoideus muscle originates either on the inner surface of the clavicle and cleithrum (*Polypterus*, Jessen 1972 : pl. 16, figs 1, 2), or is continuous with the ventral body musculature (*Acipenser*, Jessen 1972 : pl. 13, fig. 1) and did not attach to the pectoral girdle. In teleosts the clavicles are lost; the sternohyoideus muscle originates on the outer surface of the elongated ventral arm of the cleithrum (*Elops*, Jessen 1972 : pl. 7, fig. 4) or again is continuous with the ventral body musculature (*Salmo*, Jessen 1972 : pl. 15, fig. 1). In *Lepisosteus* and *Amia* the sternohyoideus muscle has a similar area of origin to that of *Elops*. Two or three elongated plates of bone, bearing scattered denticles and patches of ganoine, are embedded in the skin covering this muscle in *Lepisosteus* (Liem & Woods 1973 : pl. 4b); Jarvik (1944) considered these plates homologous with the clavicles of chondrosteans. Since both lie lateral to the sternohyoideus muscles, this seems likely. If the identification is correct, there is no doubt that the serrated plates and appendages of *Amia*, *Caturus* and *Propterus* are derived from the clavicle too. However, in *Lepisosteus*, additional bony plates may occur on the cleithrum (Fig. 51). They are much smaller than the two or three large plates described by Jarvik, which they resemble in bearing denticles and ganoine. The smaller plates lie alongside the larger plates, and in the skin covering the dorsal arm of the cleithrum. Thus bony plates are able to form in the dermis over a large area of the cleithrum and it is by no means clear that this ability is derived from the ability to form the clavicle of chondrosteans.

Whatever the homologies of the serrated appendage in *Propterus*, its presence cannot be taken as evidence of relationship with the amiid–caturid group until the distribution and form of this element is more widely known among the Neopterygii. Although suggestions have been made (Wilder 1876 : 259, Wright 1884, Liem & Woods 1973), the functions of the serrated appendage remain a mystery.

(ix) Dorsal and anal fins. The macrosemiids are remarkable in possessing a long dorsal fin. This feature was probably acquired independently by the family, although elongated dorsal fins occur in other non-teleosts. They are present in amiids (*Amia*), caturids (*Macrepistius*, *Ophiopsis*) and, in association with a deep body, in pycnodonts, platysomid chondrosteans and some

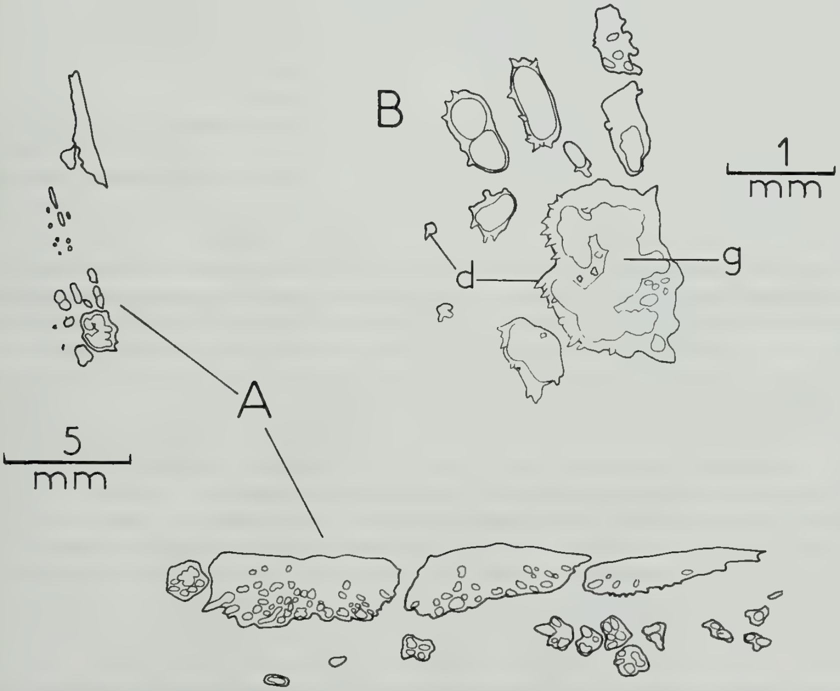

Fig. 51 *Lepisosteus osseus* (Linnaeus). A, denticle-bearing plates in skin over cleithrum of right side. B, upper plates enlarged.

'semi-onotids' (*Dapedium*). *Histionotus*, *Propterus* and *Notagogus* are the earliest known actinopterygians in which the dorsal fin is divided.

The single dorsal fin of *Macrosemius* resembles that of *Amia calva* and was probably used in a similar way. During rapid locomotion, *Amia* folds down the anterior part of the dorsal fin, the posterior part remaining erect and supplementing the thrust produced by the rounded caudal fin (personal observation). That *Macrosemius* used the dorsal fin in a similar way is suggested by the large, rounded form of the anal fin which presumably balanced the thrust. Slow locomotion in *Amia* is effected by the passage of waves along the dorsal fin while the trunk is held straight; these waves may pass fore or aft. During braking the pectoral fins are held vertically, and their action is supplemented by the dorsal fin, which is thrown into forwardly-passing waves. Harris (1937), and see Patterson's (1964 : 451) discussion, drew attention to the fact that pectoral fins placed low on the body, such as those of *Amia*, would tend to pitch the fish if they were used as brakes. A long dorsal fin may be used to counteract this tendency.

The leading rays of the first dorsal fin in *Propterus* and *Histionotus* are greatly elongated, whereas those following decrease rapidly in height. The leading anal fin-rays of these genera are also long; such fins are unknown in other non-teleosts, and their significance is not clear. Perhaps these fins were capable of erection and depression and served as releaser stimuli to other individuals, for example during territorial or sexual display.

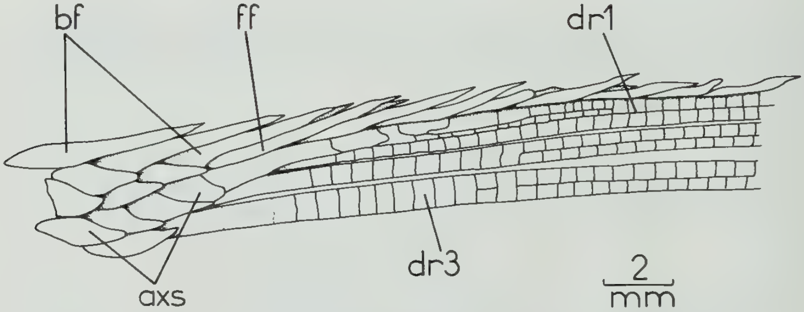

Fig. 52 *Lepisosteus osseus* (Linnaeus). Uppermost fin-rays of caudal fin viewed from the left.

(x) Caudal fin. The caudal fins of macrosemiids are primitive in at least two respects: epaxial fin-rays are absent, and there is no sharp distinction between the uppermost ray and the axial lobe squamation.

Epaxial fin-rays, articulating with epurals and preural neural spines, are a specialization shared by many groups (pholidopleurids, pycnodonts, amiids, teleosts, pachycormids, saurichthyids) but I do not think they are indicative of relationship, as Patterson (1973 : 297) suggests.

Unlike the other axial lobe rays, the uppermost does not insert beneath the squamation proximally, but remains superficial, and is not sharply delimited from the axial lobe scales. A similar phenomenon occurs in *Lepisosteus*, in which the uppermost ray clasps the tip of the notochord (Fig. 52); in contrast, the remaining axial lobe rays penetrate beneath the squamation and clasp the hypurals. Among 'semionotids' the longest axial lobe scale-row continues wholly (*Acentrophorus varians*) or partly (*Dapedium orbis*) along the uppermost ray (Gill 1923 : figs 15, 16). In some pholidophorids too the reduced uppermost ray has remained superficial (Patterson 1968 : fig. 3), and in a species of *Caturus* with cycloid scales (BM(NH) 37095) the uppermost ray does not penetrate beneath the urodermals, unlike its deeply-clasping successors (personal observation). Since the fin-rays were presumably primitively scale-like and superficial, as they are in *Aeduella* (Heyler 1969 : 192), the retention of scale-like characters by the uppermost ray is likely to be a primitive actinopterygian character, and no indicator of relationships.

The caudal fins of macrosemiids are remarkable for the constancy of number of the eight lower, non-axial lobe rays. Variation in caudal fin-ray number occurs only in the axial lobe rays; there are eight of these in *Histionotus*, 7–8 in *Propterus*, 5–6 in *Legnonotus*, 4–6 in *Notagogus* and 3–5 in *Macrosemius*. As in teleosts (Marshall 1971 : 32, Gosline 1969 : 162), a low caudal fin-ray number is associated with weakly-forked or rounded fins. Thus in *Histionotus*, the two lobes of the deeply-forked fin are each supported by eight rays, whereas the single rounded lobe of *Macrosemius* is supported mainly by the eight lower rays. A similar predominance of the lower rays appears to occur in the rounded caudal fin of *Dapedium pholidotus* (Wenz 1968 : fig. 38). Unfortunately too few reliable drawings of the caudal fins of chondrosteans and holosteans have been made; it would be interesting to know the relationship of the caudal fin-rays, the axial lobe and its scales and the termination of the lateral line in various groups.

(xi) Squamation. Schultze (1966) has made a comparative study of the scales of neopterygians. Both *Amia* and living teleosts possess cycloid scales. These are thin, flexible, rounded in outline and deeply overlapping; ganoine and peg-and-socket articulations are absent. Schultze distinguishes between those of *Amia* (Amiiden-Rundschuppe) and those of the teleosts; the surface of the former is raised into radial ridges, and that of the latter into concentric ridges. Although most macrosemiids have rhomboid scales, at least in the adult, both *Enchelyolepis* (Schultze 1966 : fig. 34) and young individuals of ? *Notagogus pentlandi* (Schultze 1966: 276) have cycloid scales with a radiating ornament on the overlapped surface. For several reasons, however, this cannot be taken as evidence of relationship between macrosemiids and halecomorphs.

According to Kerr (1952 : 68), the radiating ridges on the scales of *Amia* are due to the fusion of 'calcified rods'. At the periphery of the overlapped part of the scale 'the rods lie free, losing their calcification and ending as homogenous knobs of collagen immediately below the epidermis'. The periodic bending of the rods is 'the result of a twisting within the substance of the collagen sheet' in which they originate. The fused rods are underlain by a non-mineralized fibrous layer. In a young specimen of *Caturus* sp. (BM(NH) P44900), the overlapped portion of the scale is also formed of fine rods, free from each other along most of their length and exhibiting periodic bending, as in *Amia*. These were stabilized by the underlying fibrous layer which in this specimen had just begun to mineralize. In older specimens of *Caturus* (Schultze 1966 : figs 3a, b, 51) the rods are fused together (forming the 'Knochenschicht'), and the fibrous layer ('Faserschicht') becomes fully calcified. In the primitive teleost *Leptolepis* (Schultze 1966 : fig. 50) the scales when examined in section are seen to be very similar to those of *Caturus*; the main difference between the two lies in the pattern of surface ridges. That there is no fundamental distinction between the two types of cycloid scale is suggested by several facts. Thus Schultze has shown that in several holosteans with rhomboid scales (*Macrosemius*, *Pholidophorus*, pachycormids), the bony layer of the scale beneath the ganoine displays both radial and concentric markings. Further, in the pholidophorid *Pholidophoropsis* (Schultze 1966 : 278) cycloid scales are present with radial ridges. Finally, in the chondrostean genus *Coccolepis*, cycloid scales with both types of marking occur. *C. woodwardi* Waldman displays scales with concentric ridges (Waldman 1971 : pl. 2, fig. 4), or with fine sinuous radii (pl. 2, fig. 5). Waldman writes of the latter: 'on reaching the margin of the scale, the radii protrude over the edge by a minute amount. These protrusions would probably have been embedded in tissue.' This condition is very similar to that which occurs in *Amia* and *Caturus*.

Thus the ability to form cycloid scales of the *Amia*-type is not confined to fossil relatives of this genus, and thus their occurrence in the Macrosemiidae gives no indication of relationship between the two groups. The presence of cycloid scales in young ? *Notagogus* (they are rhomboid in the adult) is a possible indication that such scales are the first to be formed in other actinopterygians with rhomboid scales; thus the appearance of cycloidy in the adults of diverse groups (halecomorphs, teleosts, palaeoniscids such as *Cryphiolepis*, *Disichthys* and *Coccolepis*) may be due to the retention of a juvenile character, rather than to the evolution of a new one.

The squamation of *Macrosemius* displays two features of special interest: secondary scale-rows intervening between the regular transverse rows above the lateral line (found also in *Uarbryichthys*), and a lack of scales in a wide strip on either side of the dorsal fin (occurring in *Legnonotus* too). Secondary transverse rows are rare; among chondrosteans they may occur close to the dorsal and anal fins, as in *Bourbonella* ('écailles de transition'; Heyler 1969 : fig. 113) and *Paramblypterus* (Blot 1966 : fig. 17), or at the base of the axial lobe of the caudal fin (Hutchinson 1973 : 331). In the halecostome *Aphanepygus*, secondary scale-rows occur on the cheek and across the entire width of the trunk in the anterior region. In this form, the secondary scales are more numerous than those of the adjacent primary rows, from which they also differ in shape. Although this genus was placed in the Macrosemiidae by Bassani (1879), there is no sound evidence to support its retention within this family (Bartram 1977).

Areas of trunk devoid of scales occur in diverse fossil groups. Scales may be absent from the entire body with the exception of the axial lobe, as in the palaeoniscoids *Birgeria* and *Carboveles*, or from the posterior half of the trunk, as in the pycnodont *Macromesodon* and the 'semionotid' *Hemicalypterus* (Schaeffer 1967 : fig. 12). Apart from *Macrosemius* and *Legnonotus*, only '*Macrosemius*' *maeseni* (Saint-Seine in Saint-Seine & Casier 1962 : fig. 2) displays a scale-free area confined to a strip on either side of the dorsal fin. This fish probably belongs to the chondrostean genus *Tanaocrossus* Schaeffer (see p. 207). The regions on either side of the dorsal and anal fins are the last to form scales in ontogeny; among fish with rhomboid scales, scale-free areas in these locations have been found in juveniles of *Parasemionotus labordei*, *Pteronisculus cicatrosus* (Lehman 1952 : pl. 33a, c) and in the teleost *Wadeichthys oxyops* (Waldman 1971 : 30; pl. 16).

Thus the squamation of the macrosemiids offers no evidence of relationship with other neopterygian groups apart from *Uarbryichthys*.

The Macrosemiidae in relation to other Actinopterygians

Of the families of fossil actinopterygians recognized today, Thiollière's Macrosemiidae was among the earliest to be founded. In a summary of his conclusions following work upon the Jurassic fishes of Cerin (Thiollière 1858 : 782) he accepted Agassiz's family of the pycnodonts, while rejecting those of the sauroids and lepidoids. Thiollière recognized the need for a more 'natural' classification of the genera forming the last two groups, and noted that Pictet (1850) had begun well in erecting the family Leptolepidae. He proposed to establish a third family, the Macrosemiidae, 'qui réduira un peu le nombre de ces formes génèriques encore flottantes'.

He listed the genera forming the new family as *Macrosemius*, *Disticholepis* (= *Macrosemius*), *Histionotus*, *Notagogus*, *Propterus*, *Legnonotus* and *Rhynchoncodes* (= *Propterus*). These forms were considered by Thiollière to resemble one another in the structure of the skull, the form of the body, and in having an elongated dorsal fin. As is shown below, there is little doubt that the genera listed by Thiollière constitute a monophyletic group.

Woodward (1895) dealt with the phylogeny of the macrosemiids. He added the genus *Ophiopsis* to the family for the first time, and wrote of this form (**3** : 166): 'This is the least specialised genus ascribed to the Macrosemiidae and may be regarded as a link between this family and that of the Eugnathidae.' While *Ophiopsis* resembles the caturids, Woodward does not make clear his reasons for including this genus within the macrosemiids; they possess in common a long dorsal fin and a marked curvature of the mandible, and presumably he considered that these indicate relationship between the two.

Subsequent authors have all accepted in their classifications the link between *Ophiopsis* and the Macrosemiidae *sensu* Thiollière, and thus between the Macrosemiidae *sensu* Woodward and the caturids (Rayner 1941, Saint-Seine 1949, Berg 1955, Arambourg & Bertin 1958, Danil'chenko 1964, Lehman 1966, Romer 1966, Gardiner 1967, McAllister 1968).

Patterson (1973), in the knowledge that the present work was in progress, omitted the Macrosemiidae from his scheme of holostean and teleostean relationships. In his classification, Patterson has attempted to express the hierarchy of phylogenetic relationships within the non-chondrostean actinopterygians (Neopterygii). This has involved the definition of monophyletic groups in terms of specialized characters believed to have been commonly derived. If, as in the case of caturids and pholidophorids, no such specializations can be found, the paraphyletic nature of the group is admitted. The cladistic approach towards classification replaces the traditional typological identification of groups. The latter approach, based upon general resemblances shared by groups, is useless as a means of detecting relationships between them. When a typologically-recognized group, such as the Macrosemiidae *sensu* Thiollière, can be defined as a monophyletic group by the possession of shared specializations, this correspondence cannot be taken as a vindication of the typological approach. Rather, it must be treated as a special case, because the group is rich in derived characters.

Patterson's (1973) classification may be summarized as follows. He can find no evidence to suggest that *Lepisosteus* is descended from a group of fishes with a mobile maxilla or an interopercular; he places this genus in the division Ginglymodi, the sister-group of, and thus equal in rank to, the division Halecostomi, comprising the holosteans and teleosts. The halecostomes form two large sister-groups: the Halecomorphi (*Amia* and its fossil relatives), and the Teleostei (Recent teleosts and their fossil relatives). The relationships of the 'semionotids', probably a polyphyletic group, are unclear; they share none of the specializations of the halecomorphs or teleosts, and are considered to be basal halecostomes. Patterson stresses that the holosteans and teleosts need to be known in much greater detail before such a scheme can be accepted with confidence. Nevertheless his classification is used here as a working hypothesis, since it is sounder in method and wider in scope than any other.

The radical view of Jessen (1972), that the chondrosteans are more closely related to the teleosts than are the holosteans, is not accepted here. The implications that follow from it are most unlikely; either the chondrosteans retained mostly primitive actinopterygian characters (except in the pectoral girdle) and the holosteans and teleosts evolved in parallel to an improbable extent, or the many characters shared by holosteans and teleosts are primitive and those of the chondrosteans derived. These alternatives are equally unacceptable on present evidence.

There is no doubt that the macrosemiids are neopterygians. They display the following neopterygian specializations as identified by Patterson (1973).

1. Axial lobe of tail reduced.
2. Fin-rays equal in number to their supports in dorsal and anal fins.
3. Premaxilla immobile with a nasal process lining the nasal pit.
4. Vomer present.
5. Articular with a coronoid process.
6. Suspensorium upright and preopercular with a narrow dorsal arm.
7. Symplectic present.
8. Clavicles reduced.

Macrosemiids exhibit 21 specializations relative to the primitive neopterygian condition. The first two following are unique among actinopterygians and indicate that the Macrosemiidae *sensu* Thiollière constitute a monophyletic group; the genera in which each specialization is known to be present are given in parentheses. The genera *Ophiopsis*, *Songanella*, *Aphanepygus* and *Uarbryichthys*, which have been placed in the Macrosemiidae since Thiollière's publications, share neither of these specializations.

1. Nine infraorbitals, of which the first seven are scroll-like and the two behind the eye tubular. (*Macrosemius*, *Propterus*, *Histionotus*.) Although mormyriform teleosts have infraorbitals of similar shape, there are fewer than in the macrosemiids (Taverne 1971).

2. Interopercular small and remote from the mandible. (Known in all genera except *Legnonotus* and *Enchelyolepis*.) In all other groups the anterior end of the interopercular maintains a close proximity to the hind end of the lower jaw.

Macrosemiids share the following specializations with the Ginglymodi (*Lepisosteus*).

3. Absence of the opisthotic. (*Macrosemius*.) This is not unique; it is absent too in the halecostomes *Lepidotes*, *Amia* and the post-pholidophorid teleosts (Patterson 1975).

4. Extension of the exoccipital beyond the vagus canal. (*Macrosemius*.) This character also occurs in *Lepidotes* and post-pholidophorid teleosts (Patterson 1975).

5. Absence of the gular. This bone is also absent in *Acentrophorus*, *Lepidotes* and in all Recent teleosts except *Albula*, *Megalops* and *Elops*.

The macrosemiids possess none of the specializations of *Lepisosteus* identified by Patterson (1973 : 262) as unique (holospondylous, opisthocoelous centra; teeth with plicidentine; supraorbital canal running through premaxilla; a chain of toothed infraorbital bones). In contrast the macrosemiids share the following specializations with the Halecostomi, the sister-group of the Ginglymodi.

6. Mobile maxilla with a peg-like process anteriorly. (Known in all genera except *Legnonotus* and *Enchelyolepis*.)

7. Interopercular present.

8. Presence of uncinate processes on epibranchials. (*Macrosemius*.)

These specializations indicate that macrosemiids are halecostomes. Patterson (1973 : 262) identified several more halecostome specializations which are shared by teleosts (at the pholidophorid level) and halecomorphs. It is not known whether macrosemiids have a large posterior myodome or a large post-temporal fossa; both of these are present in *Lepidotes* and *Dapedium* too. Neither is it known whether the intercalar of Macrosemiidae has a membranous component. Two advanced halecostome characters are known to be missing in macrosemiids, however; these are the presence of a supramaxilla, and the loss of the quadratojugal as an independent element. Among halecostomes only *Acentrophorus* has no supramaxilla, and there is no evidence to suggest that its absence in macrosemiids is other than primitive. In all halecomorphs except *Furo longiserratus* (see p. 212) the quadratojugal is reduced to a small process on the quadrate or is absent altogether (*Amia*), and in teleosts the bone forms a splint-like outgrowth of the quadrate. The presence of an independent quadratojugal in a species of *Furo* suggests that it was independent too in the common ancestor of halecomorphs and teleosts, and that it became fused to the quadrate in parallel in these two groups. Thus the presence of an autogenous quadratojugal in macrosemiids (found also in *Lepisosteus*, *Lepidotes* and *Dapedium*; Patterson 1973) does not debar this group from membership of either the halecomorphs or teleosts. But the absence of a supramaxilla suggests that the macrosemiids belong to neither subdivision and are basal halecostomes. This may be tested by asking whether the macrosemiids possess the specializations which define the halecomorphs and teleosts each as monophyletic groups.

According to Patterson (1973 : 287) there is only one specialization unique to the Halecomorphi (Parasemionotidae, Caturidae and Amiidae), namely the articulation between the symplectic and the lower jaw. The available material reveals no such articulation in the macrosemiids. As Patterson (1973 : 248–250) points out, this character is not definitely an advanced one since the small bone in contact with the quadrate region of the palate and with the hind end of the mandible in palaeoniscids may be a symplectic, as identified by Nielsen (1942 : figs 35, 36, 70). If this character is invalid as a specialization then the parasemionotids cannot be included within the halecomorphs. However, the remaining halecomorphs (Amiidae and Caturidae) do share unique specializations. Thus in *Amia*, *Caturus heterurus*, *Heterolepidotus* and *Macrepistius* the dermosphenotic is incorporated into the skull roof and enwraps the front surface of the sphenotic. Although the dermosphenotic forms part of the skull roof in *Notagogus* it has no enwrapping flange, and in other macrosemiid genera this bone appears to have been hinged to the skull roof. Another important halecomorph specialization is the form of the intercalar. In *Amia* and in caturids where the braincase is known this bone forms membranous outgrowths which extend over the outside of the saccular chamber (Patterson 1973 : 280). Unfortunately this region of the braincase remains unknown in macrosemiids.

Thus there is no evidence at present which indicates relationship of the macrosemiids to the Halecomorphi. There is good evidence, however, that *Ophiopsis*, which does not belong in the Macrosemiidae, is closely related to the well-known caturid *Macrepistius* (Bartram 1975).

Patterson (1973) has marshalled an impressive set of unique specializations which define teleosts and their fossil relatives as a monophyletic group (Teleostei *s. str.*). These occur at the pachycormid level and involve the snout region, the quadrate and associated bones, and the caudal endoskeleton.

Primitively, teleosts have small, mobile premaxillae associated with bones Patterson has named lateral dermethmoids. As described in the preceding section, the primitive neopterygian premaxilla is immovably fixed to the braincase by a stout nasal process; this may encircle the olfactory nerve. In teleosts, in contrast, the premaxillae are small and mobile and the nasal processes are represented by separate lateral dermethmoid bones which in pholidophorids may also encircle the olfactory nerve. Primitively, as in *Pachycormus* and certain pholidophorids, these elements bear teeth. In pachycormids and living teleosts the lateral dermethmoids fuse with the rostral forming a rostro-dermethmoid; in higher teleosts this bone becomes incorporated into the mesethmoid. In the Macrosemiidae the premaxillae form nasal processes which are sutured with the braincase, and thus do not display the teleostean specialization.

In teleosts the quadratojugal forms a spine on the quadrate, the two receiving the symplectic in a groove along the inner surface. Although fusion occurs between quadratojugal and quadrate in some macrosemiids, in none is the quadratojugal as completely united with the quadrate as it is in Recent teleosts or even in pholidophorids. Although the symplectic of macrosemiids is not surely known, in *Macrosemius* at least no groove is formed for it on the inner surface of the quadrate.

The teleosts are unique in having uroneurals, neural arches which have elongated to stiffen the caudal fin. Patterson has found them in all groups usually related to the teleosts (at least those in which the caudal endoskeleton is known), and in the Pachycormidae. The caudal endoskeleton of macrosemiids is known only in two specimens of *Enchelyolepis*; these are very small and may be immature. However, they provide no evidence of uroneurals; the neural arches are small and scarcely ossified, in contrast with the stout, median, epurals.

Thus the Macrosemiidae show no evidence of relationship to either the teleosts or halecomorphs and so must be considered to be basal halecostomes.

The remaining specializations relative to the primitive neopterygian condition which the macrosemiids display are as follows.

9. Preopercular sensory canal exposed by large fenestrae at the base of the dorsal arm and along the entire length of the lower arm of the preopercular. The preopercular canal is similarly exposed in many teleosts (*Albula*, *Gymnarchus*, *Notopterus*, for example).

10. Supratemporals reduced and excluded from the midline; the medial part of the supratemporal commissure is borne by the parietals, which have probably fused with the medial supratemporals. (*Macrosemius*, *Propterus*, *Histionotus*.) This condition is found in many teleosts (McDowell 1973 : 12).

11. Frontals constricted in the preorbital region of the skull and housing the supraorbital canal in a gutter. (Known in all genera except *Enchelyolepis*.) This condition is very common in several groups of teleosts.

12. Nasals scroll-like. (*Macrosemius*, *Propterus*.) This condition is again found in many teleosts.

13. Suborbitals absent. Suborbitals have also been lost within the halecomorphs (*Amia*) and within the teleosts (all post-pholidophorid teleosts; Patterson 1973).

14. Hyomandibular bearing lateral flange. (*Macrosemius*, *Propterus*, *Histionotus*.) Such a flange is also present in *Perca* (Osse 1969).

15. Jaw articulation below the front of the orbit. (All macrosemiids.) This character appears in most neopterygians with short jaws (*Lepidotes*, *Pleuropholis*, *Megalops*, *Chanos*).

16. Lower margin of mandible concave in lateral view. (All macrosemiids.) A less marked curvature of the lower jaw is also found in *Ophiopsis*, the zeiform *Capros* and in mormyrids.

17. Mandibular sensory canal housed in wide gutter in the dentary and angular. (All macrosemiids.) Mormyrids and many other teleosts display this feature.

18. Upper branchiostegals acinaciform. (*Macrosemius*, *Propterus*.) Acinaciform branchiostegals are widespread among acanthopterygian teleosts (McAllister 1968 : pls 11–19).

19. Proximal ceratohyal short and deep posteriorly. (*Macrosemius*, *Propterus*, *Notagogus*.) The ceratohyal is similar in mormyrids and many acanthopterygians (McAllister 1968 : pls 11–19).

20. Serrated appendage present. (*Propterus*.) Such an appendage is also known in *Amia* and *Caturus*; it is absent in teleosts.

21. Dorsal fin very long. This character is found in many groups (Amiidae, 'Semionotidae' and many teleost families).

In summary, the Macrosemiidae are a group of neopterygians which display 21 specializations, listed above, relative to the primitive neopterygian condition. The first two of these are unique and indicate that the macrosemiids form a monophyletic group. *Ophiopsis*, *Songanella*, *Aphanepygus* and *Uarbryichthys* do not have them, and are thus not included within the family. Owing to scarcity of specimens and mode of preservation, these two specializations are not known to be present in *Legnonotus* and *Enchelyolepis* either. Thus, strictly, they too should be excluded from the macrosemiids. *Legnonotus* shares with *Macrosemius*, however, a unique specialization, the absence of scales from the region on either side of the dorsal fin. *Legnonotus* is retained in the macrosemiids for this reason. Far less confidence can be had in the retention of *Enchelyolepis* within the macrosemiids, although having re-examined the specimens I feel that Woodward was right in placing them within that family. *Enchelyolepis* is retained here in the Macrosemiidae until more information is available.

In spite of this study, knowledge of the structure of the Macrosemiidae remains far from complete. This lessens the chances of accuracy in placing the group in a phylogenetic classification. Much more needs to be known, for example, about the braincase and the caudal fin, and hopefully, despite the scarcity of suitable material, these structures will eventually be described.

What is known about the macrosemiids, however, indicates that this family arose before the divergence of the halecomorph and teleost halecostomes. Since they show no evidence of relationship to any other holostean group, they have been classified here as Halecostomi, subdivision *incertae sedis*. The snout and jaw articulation of macrosemiids both display the primitive neopterygian condition, and if *Enchelyolepis* is indeed a macrosemiid, so too does the caudal endoskeleton. It is perhaps surprising then to find that so many macrosemiid specializations are also found in teleosts. But some of these (11–13, 17, 19 above) are evidently due to a tendency within the family to lose laminar bone, while others (10, 14) are due to the relative shortness of the postorbital region of the skull, or (15, 20) to the shortness of the jaws.

Relationships within the Macrosemiidae

The macrosemiids present a variety of form unusual among holostean groups. By analysing these variable characters, the interrelationships of the genera within the family may be suggested. The following specializations occur within the Macrosemiidae:

1. Dorsal fin divided (*Notagogus*, *Histionotus*, *Propterus*). Apart from the macrosemiids and polypterids, divided dorsal fins are unknown among non-teleost actinopterygians. A long, undivided dorsal fin is undoubtedly the primitive macrosemiid condition; such a fin occurs in *Uarbryichthys*.

2. Scales absent on either side of the dorsal fin (*Macrosemius*, *Legnonotus*).

3. Ganoine on scales reduced (*Macrosemius*, *Propterus*).

4. Trunk shallow (*Macrosemius*, *Legnonotus*). There are several indications that macrosemiids were primitively deep-bodied, as are *Uarbryichthys*, *Histionotus* and *Propterus*. Both Gregory (1933 : 131) and Saint-Seine (1949 : 196) mention that the macrosemiid skull is reminiscent of those of deep-bodied fish. The origin of the family from fishes with deep bodies may also account for the presence of the elongated dorsal fin, since the two features are often associated as Gregory also points out. This association occurs in *Uarbryichthys*.

5. Caudal fin weakly forked or rounded, with a reduced number of rays (*Macrosemius*, *Legnonotus*, *Notagogus*). The tail of *Histionotus* is probably the most primitive; it is deeply forked, with the highest number of rays.

6. Surface of parietals forming stout ridges (*Histionotus*, *Propterus*). This unusual feature is unknown among other holosteans. The smooth skull roof of *Notagogus* and *Macrosemius* is undoubtedly primitive.

7. Quadratojugal notched close to distal end (*Propterus*, *Histionotus*).

8. Maxillary teeth reduced (*Macrosemius*, *Propterus*) or absent (*Histionotus*). The full row of teeth displayed by *Notagogus* and *Legnonotus* is presumably primitive for the family.

9. Reduction or loss of fringing fulcra on dorsal fin (*Macrosemius*, *Propterus elongatus*, *P. microstomus*, *Notagogus*), anal fin (*Macrosemius*, *Notagogus*) and paired fins (*Propterus elongatus*, *Macrosemius*, *Notagogus*).

10. Sensory canals in the posterior part of the skull roof large and exposed by large fenestrae (*Macrosemius*, *Histionotus*, *Propterus*). In *Notagogus* these canals are narrow and completely

enclosed; this is probably the primitive macrosemiid condition, since it is found also in *Uarbryichthys.*

11. Dermosphenotic not incorporated into skull roof and not enclosing the junction between infra- and supraorbital canals (*Macrosemius, Histionotus, Propterus*).

12. Anterior dorsal fin emarginate (*Histionotus, P. microstomus*).

Characters 6 and 7 unite *Propterus* and *Histionotus*, and characters 2 and 4 unite *Macrosemius* and *Legnonotus* as monophyletic groups, with little doubt. If this is correct, then the relationship between *Notagogus* and these two macrosemiid subgroups is not easy to determine. Although this genus shares specialization 5 with *Macrosemius – Legnonotus*, it also shares specialization 1 with *Histionotus – Propterus*. But if *Notagogus* is placed in either group it demands that specializations 10 and 11 arose within the family twice, which seems unlikely. It is more reasonable then to place *Notagogus* as the sister-group of the other four genera, and assume that the divided dorsal fin and reduced caudal fin were acquired in parallel by this genus. The genus *Enchelyolepis* is too ill-known at present to be fitted into this scheme of relationships.

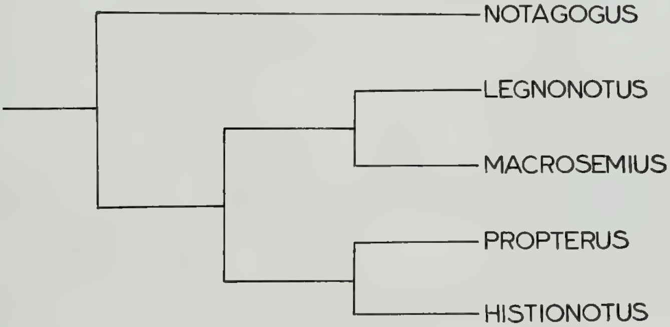

Fig. 53 Suggested interrelationships within the Macrosemiidae.

In summary, the variable characters of the macrosemiids were primitively in the following states: dorsal fin undivided; squamation entire; ganoine covering on scales entire; trunk deep; caudal fin deeply forked with at least 16 rays; surface of parietals smooth; quadratojugal without notches; oral margin of maxilla bearing full row of teeth; fringing fulcra on all fins; sensory canals on skull roof fully enclosed by bone; dermosphenotic incorporated into skull roof. All these are found primitively in Neopterygii and, with the possible exception of the maxillary teeth, in *Uarbryichthys*, the plesiomorph sister-group of the macrosemiids. *Notagogus* acquired a divided dorsal fin, a less strongly forked caudal fin, and a depressed trunk. This genus forms the sister-group of all the other macrosemiids, whose skull roof sensory canals became exposed by large fenestrae, and whose dermosphenotics became reduced. *Macrosemius* and *Legnonotus* are most closely related to each other, as indicated by the loss of the dorsal squamation. In parallel with *Notagogus*, however, these two genera acquired a depressed trunk and a reduced caudal fin; they retained the continuous dorsal fin. *Histionotus* and *Propterus* are united by the notched quadratojugal, and by the ridged parietals; they acquired divided dorsal fins in parallel with *Notagogus*, and a reduced maxillary dentition in parallel with *Macrosemius*.

Ecological note

The macrosemiids are represented in the Triassic by *Legnonotus* only, and none occur in the Lower Jurassic. Thus no members of this family formed part of the Triassic marine faunas of Italy, or of the great Lias faunas preserved at Lyme Regis and Holzmaden. Most species and specimens of macrosemiids have been recovered from Upper Jurassic and Lower Cretaceous deposits associated with reef-building organisms. Thus *Macrosemius*, *Propterus*, *Notagogus* and *Histionotus* occur in the Lithographic Limestones of Bavaria and Cerin, and *Propterus* and *Notagogus* occur too in those of Lerida in Spain. These deposits were laid down offshore under calm conditions, protected from the open sea by a barrier reef (Saint-Seine 1949, Barthel 1970). It seems that the Macrosemiidae were adapted to, and perhaps largely confined to, the reef environment; it would be surprising if none were found at the recently-discovered Upper Jurassic fossiliferous locality at Canjuers (Var, France).

According to Barthel, the floor of the Bavarian lagoon was raised into ridges formed by sponge and algal reefs. Coral reefs grew on some of these, forming the barrier which defined the lagoon. Fine calcareous particles were brought in from the open sea, and settled on its floor between the ridges. The reefs supported a large population of benthonic crustaceans; although preserved in the calcareous mud, few have left their tracks there, and Barthel takes this as evidence that conditions on the floor of the lagoon were lethal.

Two broad categories of food must have been available to the fishes in this environment. The first comprised fast-moving prey, such as cephalopod molluscs and fish. Such prey was available to large fish with highly-forked tails, small fins and a large gape armed with sharp teeth, for example *Caturus*, *Pholidophorus*, *Aspidorhynchus* and *Thrissops*. The second category includes stationary food (algae, corals, detritus) and comparatively slow-moving animals (benthonic molluscs and crustaceans). Such food would have been taken by fishes with small mouths, moving relatively slowly and relying on the reefs for shelter from predators.

It seems that the macrosemiids belong with the latter group. Their small gape, reduction of the maxillary teeth and stoutness of the remaining dentition indicate that these fishes took algae or small armoured prey. The large surface area of the fins of macrosemiids suggests that they moved slowly but with great manœuvrability through the reefs. The stout sharp basal fulcra on the tails of *Macrosemius* and *Propterus* would have deterred attack from the rear.

At least two examples are known of macrosemiid-as-prey. A specimen of *Ionoscopus desori* (LM 15.313) has a *Notagogus* in its abdomen, and a specimen of *Belonostomus tenuirostris* (LM 15.509) has another individual of the same genus in its jaws (Saint-Seine 1949 : 182; pl. 24, fig. C).

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Explanation of abbreviations used in text-figures

Adp	anterior dermopalatine
Ang	angular
Ant	antorbital
ap	ascending process of parasphenoid
apl	anterior pit-line on parietal
Art	articular
axs	scales of axial lobe of caudal fin
bf	basal fulcrum
Boc	basioccipital
bpr	basipterygoid process of parasphenoid
Brr	branchiostegal ray
c	centrum
cbr	ceratobranchial
cc	position of crus communis of membranous labyrinth
Cl	cleithrum
Cor	coronoid
D	dentary
d	denticle
Dch	distal ceratohyal
Dpt	dermopterotic
dr	ray emanating from axial lobe of caudal fin
Dsp	dermosphenotic
E	ethmoid ossification
ebr	epibranchial
ec	ethmoidal commissural sensory canal
Ecp	ectopterygoid
Enp	endopterygoid
ep	epural
Epo	epioccipital
epsa	foramen for efferent pseudobranchial artery
Exo	exoccipital
F	frontal
fapf	foramen for anterior palatine ramus of facial nerve
ff	fringing fulcrum
fib	facet on epibranchial for articulation of pharyngobranchial
fm	foramen magnum
gac	groove on prearticular receiving process of coronoid
glf	glossopharyngeal foramen
gs	glenoid articulatory surface of mesocoracoid arch
h	hypural
Hb	hypobranchial
Hh	hypohyal
Hm	hyomandibular
hsc	horizontal semicircular canal
Ih	interhyal
Io	infraorbital
ioc	infraorbital sensory canal
Iop	interopercular
Las	lateral anal scale
lcc	lateral cranial canal
lf	lateral flange of hyomandibular
lp	lateral process of fin-ray
mc	mandibular sensory canal
Mco	mesocoracoid arch
mefc	foramen for external mandibular ramus of facial nerve
mll	main lateral line
mp	medial process of maxilla
mpl	middle pit-line on parietal
Mpt	metapterygoid
mr	middle segment of dorsal fin radial
Mx	maxilla
N	nasal
np	nasal process of premaxilla
Op	opercular
Ors	orbitosphenoid

P	parietal
pall	pit of accessory lateral line
Pans	postanal scale
Pas	parasphenoid
Pch	proximal ceratohyal
Pdp	posterior dermopalatine
Pmx	premaxilla
Pop	preopercular
Pos	preanal scale
pp	pedicel on parasphenoid
pr	proximal fin radial
Pra	prearticular
Pro	prootic
Prop	propterygium of pectoral fin
psc	posterior semicircular canal
Pte	pterosphenoid
Pto	pterotic
ptsr	primary transverse scale-row
Ptt	post-temporal
pu	preural centrum
puhs	preural haemal spine
Q	quadrate
Qj	quadratojugal
R	rostral
r	fin-ray

Rar	retroarticular
S	symplectic
sac	position of sacculus
Sang	surangular
Scl	supracleithrum
Ser	serrated appendage
So	supraorbital(s)
soc	supraorbital sensory canal
Sop	subopercular
Sph	sphenotic
spl	splint(s) preceding leading fin-ray
stc	supratemporal commissural sensory canal
stsr	secondary transverse scale-row
Stt	supratemporal
tp	transverse process of centrum
ud	urodermal
up	uncinate process on epibranchial
V	vomer
vp	ventral process of fin-ray
IX	glossopharyngeal foramen
X	vagus foramen

Index

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M. K. Howarth

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Abstract

The Upper Lias of Northamptonshire is redescribed from a now obscured exposure of the 3 m of limestones and clays, up to the Upper Cephalopod Bed, that could formerly be seen above the Marlstone Rock Bed in a quarry near Byfield, and from Beeby Thompson's descriptions and collections from the overlying 50 m of clays that were exposed in numerous 19th-century brickpits around Northampton. The three lowest subzones of the Upper Lias occur in the top 1 m of the Marlstone Rock Bed. This is overlain by the Transition Bed of Semicelatum Subzone age and the Abnormal Fish Bed of Exaratum Subzone age. Overlying clays and the Lower Cephalopod Bed belong to the Falciferum Subzone, followed by more clays and the Upper Cephalopod Bed belonging to the Commune Subzone. The latter subzone continues into the basal 5 m of the Unfossiliferous Beds, the middle 15 m do not contain fossils, and the top 5 m and the overlying 27 m of *Leda ovum* Beds belong to the Fibulatum Subzone. The Northampton Sand ironstone of Opalinum Zone age follows after a large non-sequence.

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It is shown that the stratigraphical range of *Zugodactylites braunianus* occurs wholly within the range of *Peronoceras fibulatum*, so the Braunianus Subzone, proposed by Thompson and Buckman as a subzone above the Fibulatum Subzone on the basis of this Northamptonshire succession, has to be abandoned. This relationship between *Peronoceras* and *Zugodactylites* is confirmed by new discoveries in Yorkshire. The Fibulatum Subzone is extended up to include the closely related genus *Porpoceras*, occurring in the Upper *Leda ovum* Beds and in a similar stratigraphical position in Yorkshire, and it is proposed to use *Catacoeloceras crassum* as the index ammonite for the top subzone of the Bifrons Zone.

The Dactylioceratidae of Northamptonshire are described, including the new species *Dactylioceras* (*Orthodactylites*) *semiannulatum* from the Exaratum Subzone, the rich faunas of *Peronoceras* and *Zugodactylites*, including the new species *Z. thompsoni*, from the Unfossiliferous and Lower and Middle *Leda ovum* Beds, and *Porpoceras* from the Upper *Leda ovum* Beds. Lectotypes for *Peronoceras fibulatum* (J. de C. Sowerby 1823), *Zugodactylites braunianus* (d'Orbigny 1845) and *Z. pseudobraunianus* (Monestier 1931) are designated. The view is again put forward that a meaningful classification of Dactylioceratidae can only be based on accurate stratigraphical knowledge of the forms and allowance for the wide variation that occurs in some characters, and it is reiterated that no good evidence for sexual dimorphism has yet been found in the family.

Introduction

The closure in 1965 of the old East and West Junction Railway, between Stratford-on-Avon and Towcester, led to the abandonment of the Marlstone Rock Bed iron-ore quarry at Iron Cross Farm, 1·5 km north of Byfield, west Northamptonshire. The tips of overburden were bulldozed back over the whole quarry, thus obliterating the last good exposure of the Upper Lias in Northamptonshire and palaeontologically the most interesting inland exposure of the Upper Lias in England. The main interest lay in the magnificent and well-preserved ammonite fauna of the Abnormal Fish Bed, a 0·15 m (6 in) bed of limestone of Exaratum Subzone age welded to the top of the Marlstone Rock bed. This Bed had been exposed for many years over a length of about 200 m at the side of the mineral railway serving the quarry, and in 1962 and 1963 a collection of about 300 ammonites was made, which included fine specimens of several species that are poorly known elsewhere in Britain. It is a matter for regret that this last good exposure of the Abnormal Fish Bed was not brought to the attention of the Nature Conservancy for possible preservation as a geological Site of Special Scientific Interest.

As well as the Marlstone Rock Bed and its contiguous Transition Bed and Abnormal Fish Bed, the Iron Cross Farm quarry also had good exposures of the overlying Lower Cepahalopod Bed and Upper Cephalopod Bed, which represented horizons up to the Commune Subzone of the Bifrons Zone. Higher beds of the Upper Lias were not seen at Byfield, but they were formerly well exposed in a series of brickpits in and around Northampton. They consist of a thick series of clays up to 50 m (160 ft) thick, the Unfossiliferous Beds below and the *Leda ovum* Beds above, representing horizons up to the top of the Fibulatum Subzone. There have been no exposures from which fossil collections could be obtained for many years, but when the brickpits were worked between 1850 and 1920 they yielded superb collections of ammonites that are still largely undescribed. Interest centres around the *Harpoceras–Zugodactylites* fauna of the *Leda ovum* Beds, a fauna that is very rare anywhere else in the Upper Lias of Britain. In addition, species of *Hildoceras* and *Pseudolioceras* occur in the same beds, and microconch forms of both genera are found, beautifully preserved in the clay facies, forms which are not known from any other British rocks of the same age.

The purpose of this paper is to present a unified description of the Upper Liassic succession and stratigraphical nomenclature, determinations of all the ammonites and the zonal subdivisions, and descriptions of the Dactylioceratidae. The Hildoceratidae will be described separately. Many collections of Northamptonshire Upper Lias ammonites have been examined: the two largest are Beeby Thompson's collection in Northampton Museum and the collection in the British Museum (Natural History) (prefix BM for specimen numbers) which includes good material formerly in the Dorset County Museum. Other collections are in the Geological Survey Museum (GSM) at the Institute of Geological Sciences, London, Oxford University Museum (OUM), the Geology Department of Reading University, Northamptonshire Natural History Society and Leicester City Museum.

The photographs shown in the plates were taken by the author, and the specimens were given a thin coating of ammonium chloride. All figures are natural size unless stated otherwise.

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I wish to thank Mr W. N. Terry and Northampton County Borough Council for the loan of many ammonites from Beeby Thompson's collection; also Mr Gordon Osborne of the Northamptonshire Natural History Society and Field Club, Dr H. C. Ivimey-Cook of the Institute of Geological Sciences, Mr J. M. Edmonds of Oxford University Museum, Dr S. Turner latterly of Reading University and Mr M. D. Jones of Leicester City Museum for ready access to collections in their care.

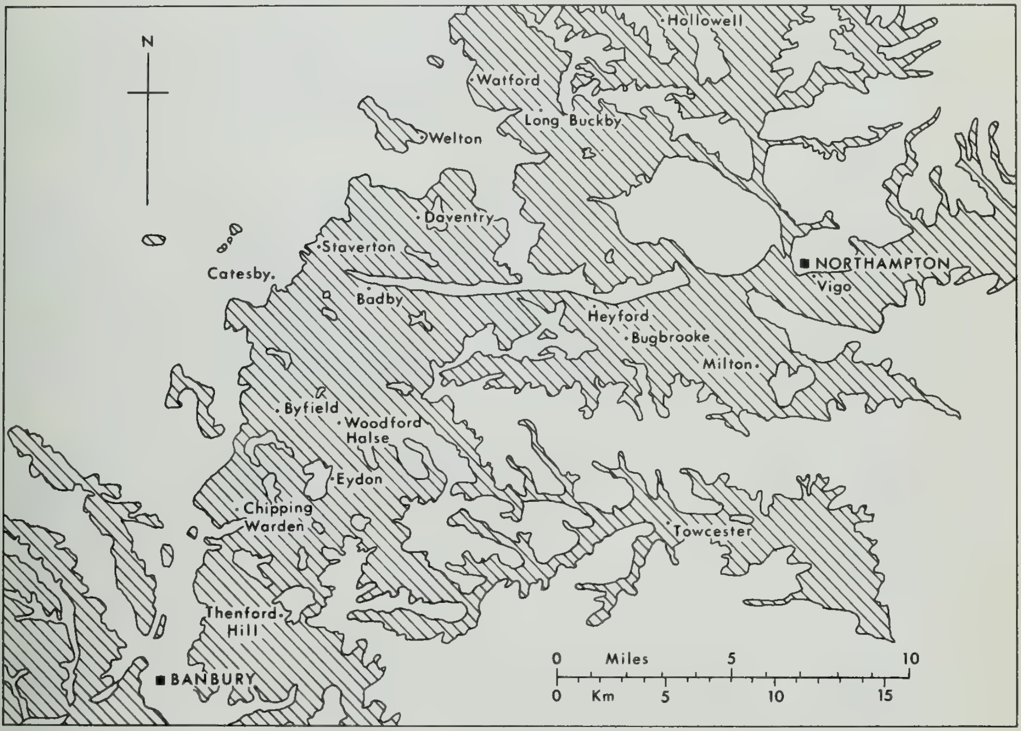
N
Hollowell
Watford
Long Buckby
Welton
Daventry
Staverton
Catesby
Badby
NORTHAMPTON
Vigo
Heyford
Bugbrooke
Milton
Byfield
Woodford Halse
Eydon
Chipping Warden
Towcester
Thenford Hill
BANBURY
0 Miles 5 10
0 Km 5 10 15

Fig. 1. Map of the outcrop of the Middle and Upper Lias (hatched) in the western half of Northamptonshire, showing all the localities referred to in the text. The Lower Lias occurs to the north-west and the Middle Jurassic to the south-east.

Stratigraphical succession

The stratigraphical succession of the Upper Lias of Northamptonshire was worked out almost single-handed by Beeby Thompson in a long series of papers between 1881 and 1910. Earlier descriptions of the Middle and Upper Lias in the neighbourhood of Banbury by Beesley (1873) and Walford (1878) had included sections at Byfield and Eydon in west Northamptonshire, and it was in their descriptions that the terms Transition Bed, Fish Bed and Cephalopod Bed originated for sections in that area. Nearer Northampton, however, no detailed description existed for the Middle and Upper Lias, and Thompson obtained his information from the numerous quarries in the Marlstone Rock Bed and brickpits in the clay facies of the Upper Lias that existed at that time. His description (Thompson 1881–86) started with the succession revealed by the quarrying of the Marlstone Rock Bed, both as iron-ore and as building stone, at about 30 localities in the western half of the county. The Transition Bed is welded to the top of the Marlstone Rock Bed, followed upwards by a variable sequence of fish beds, then the Lower and Upper Cephalopod Beds, occurring in the lowest 3·0–3·7 m of Upper Lias clays that were removed from the quarries. These represent all horizons of the Upper Lias up to the Commune Subzone of the Bifrons Zone. The beds making up the fish beds were found to be variable in development: in the western part of the county, especially around Byfield and Daventry, they are condensed into a single bed of limestone, 0·15 m (6 in) thick, welded to the top of the Transition Bed, for which Thompson's manuscript name Abnormal Fish Bed is adopted. In several places Thompson (e.g. 1892 : 340; 1910 : 463) referred to this as the 'abnormal' development of the Fish Bed, of which the 'normal' development was found in a relatively small area around Milton and Bugbrooke, 5–8 km south-west of Northampton. In spite of the number of quarries at that time, Thompson had to make excavations at both localities, and the results, presented to the British Association in 1891 (Thompson 1892 : 334–351), showed that at their maximum development the beds consisted of three limestones separated by shales or paper shales, comprising two Fish Beds below and the Inconstant Cephalopod Bed above. They were separated from the Transition Bed by paper shales up to 0·13 m (5 in) thick. The claim that the Abnormal Fish Bed was a condensed lateral equivalent of the Inconstant Cephalopod Bed and both Fish Beds is substantiated by the rich ammonite faunas now known from all of them.

The condensation at the base of the Upper Lias is greater to the south of Byfield: at Middleton Cheney and Thenford, 4–6 km east of Banbury, the Abnormal Fish Bed is thin and the Lower Cephalopod Bed occurs almost immediately above (Beesley 1873 : 23; Walford 1878 : 2; Thompson 1889 : 26–29). West and south of Banbury the Transition Bed and Abnormal Fish Bed are absent: at Wroxton and in the Neithrop cutting (Whitehead *et al.* 1952 : 148, 185; Edmunds *et al.* 1965 : 51, 59) the Lower Cephalopod Bed and clays below, both of Falciferum Subzone age, overlie the Marlstone Rock Bed directly, while at West Bloxham (Hallam 1967 : 421) the Lower Cephalopod Bed with Falciferum Subzone ammonites rests on the Marlstone Rock Bed without intervening shales.

Few descriptions of the Transition Bed to Upper Cephalopod Bed sequence have appeared since Thompson's (1910) review of the succession. Barnard (1950) described foraminifera from the shales above and below one of the Cephalopod Beds at Byfield, though he obtained his samples from new excavations in the railway cutting at Byfield itself, rather than from the excellent exposures that existed in the Iron Cross quarry 1·5 km to the north. Lord (1974 : 604) has described ostracods from the same bed in that railway cutting. The Iron Cross quarry was opened about 1920 and worked until 1965. A photograph of the vertical face, showing the Marlstone Rock Bed and the Lower and Upper Cephalopod Beds, was given by Whitehead (1952 : 159, pl. 8B). In his description of similar quarries on the west side of Byfield and at Upper Catesby (Whitehead 1952 : 177, 179), the succession at the base of the Upper Lias was not properly identified according to Thompson's nomenclature: bed at 5 Upper Catesby (: 177) and bed 4 at Byfield (: 179) are the Abnormal Fish Bed, and beds 3 and 4 at Upper Catesby and bed 3 and the top of bed 2 at Byfield are the Transition Bed. In the Banbury memoir Edmonds (1965 : 56) was equally unsuccessful in using Thompson's stratigraphical nomenclature: while the succession in the Iron Cross quarry was adequately described, the 'cream coloured earthy limestone' immediately above the Transition Bed is the Abnormal Fish Bed, and the two higher limestones are the Lower and Upper Cephalopod Beds. No comment was made on the superb ammonites in the Abnormal Fish Bed. The 'Inconstant Cephalopod Bed' (Edmonds 1965 : 51 (bed 35), 59) does not occur in the Neithrop cutting 2 km north-west of Banbury (the bed is probably the Lower Cephalopod Bed), and at Wroxton (Edmonds 1965 : 59) the two cephalopod limestones are the Lower and Upper Cephalopod Beds.

The expanded sequence of a Fish Bed overlain by the Inconstant Cephalopod Bed was seen again, for the first time since Thompson's days, in excavations below a bridge during construction of the M1 motorway in 1958, 4 km south-west of Northampton (SP 735567). Good Fish Bed and Inconstant Cephalopod Bed ammonites were collected by the author, and also ammonites from the Lower and Upper Cephalopod Beds.

After describing the 3–4 m of beds of the Upper Lias up to the Upper Cephalopod Bed, that were always found in the Marlstone Rock Bed quarries, Thompson turned his attention to the much thicker series of clays that formed the rest of the Upper Lias. They are up to 50 m thick in places, but represent only part of the Commune and Fibulatum Subzones. In Thompson's time there were about 40 pits in the clays (list in Thompson, 1910 : 465–467), though it was unusual for a thickness of more than 6 m of clays, mostly used for brick-making, to be found in any one pit. Several pits were situated within the town of Northampton itself, and a photograph of the best-known one, Vigo brickpit, accompanied Thompson's (1895 : 139–144) description of the method of working the clay. Thompson (1887–88) made four divisions, mainly by means of the different fossil constituents of the clays: the Unfossiliferous Beds at the base overlain by the Lower, Middle and Upper *Leda ovum* Beds. Beautifully preserved ammonites of the genera *Peronoceras, Zugodactylites, Porpoceras, Hildoceras, Harpoceras* and *Pseudolioceras* occur in the clay, though perhaps not abundantly, for the total number of specimens found by all collectors in the 40 exposures was only about 700. It was Thompson's discovery in these clays of species of *Peronoceras* apparently overlain by species of *Zugodactylites* that led to the proposal of the Fibulatum and Braunianus Subzones of the Bifrons Zone (Buckman 1910*a* : 86, 87; Thompson 1910 : 462). The *Leda ovum* Beds are overlain by the Northampton Sand, which has a bed of nodules at the base containing derived specimens of *Hildoceras.* Thompson always maintained that in sections undisturbed by any form of slumping the Northampton Sand followed the *Leda ovum* Beds without a break in deposition, so that the succession was complete up to the top of the Upper Lias and into the Inferior Oolite. In support of this contention he advanced innumerable arguments over a period of 40 years (Thompson 1888 : 71–73; 1890; 1893; 1896–1905; 1910 : 467; 1921; 1927), and always rejected the dating and correlations based on the ammonites. Buckman (1890) had shown at an early stage that there are no 'Jurense' Zone ammonites in the Upper *Leda ovum* Beds, and soon afterwards (Buckman 1892) he showed that the ammonites in the Northampton Sand that had been recorded as *Lytoceras jurense* belonged to Lower Bajocian, Opalinum Zone, species.

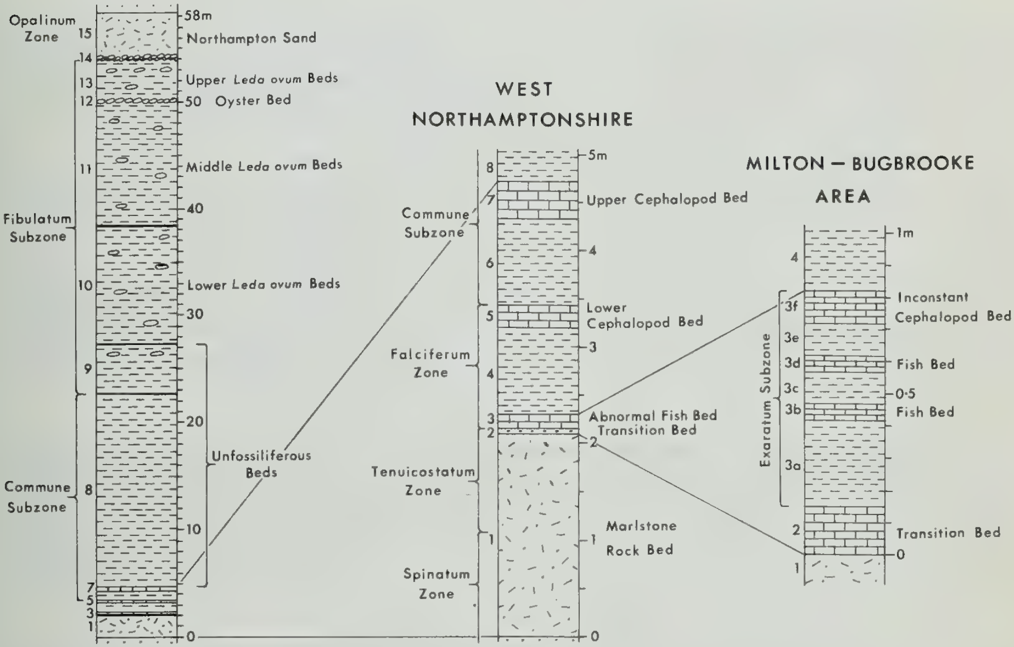
Opalinum Zone
15
14
13
12
11
10
9
8
7
5
3
1
58m
Northampton Sand
Upper *Leda ovum* Beds
50 Oyster Bed
Middle *Leda ovum* Beds
40
Fibulatum Subzone
Lower *Leda ovum* Beds
30
20
Unfossiliferous Beds
Commune Subzone
10
0
WEST NORTHAMPTONSHIRE
8
7
6
5
4
3
2
1
5m
Upper Cephalopod Bed
Commune Subzone
4
Lower Cephalopod Bed
3
Falciferum Zone
Abnormal Fish Bed
Transition Bed
2
Tenuicostatum Zone
Marlstone Rock Bed
1
Spinatum Zone
0
MILTON – BUGBROOKE AREA
1m
4
3f
3e
3d
3c
3b
3a
2
1
Exaratum Subzone
Inconstant Cephalopod Bed
Fish Bed
0·5
Fish Bed
Transition Bed
0

Fig. 2. Vertical sections of the Marlstone Rock Bed and the Upper Lias in Northamptonshire. The general section on the left (partly enlarged in the centre) shows the west Northamptonshire development of bed 3. The expanded bed 3 in the Milton–Bugbrooke area is shown on the right.

In fact, all the ammonites of the Upper *Leda ovum* Beds are indicative of the Fibulatum Subzone (as redefined here, p. 245) of the Bifrons Zone. Well-preserved specimens of *Leioceras*, such as *L. thompsoni* Buckman (1899 : xl; suppl. pl. 7, figs 13–16), occur in considerable numbers in the Northampton Sand, together with *Tmetoceras* and *Bredyia* (Thompson 1927 : 62–67), and species of *Pachylytoceras* (Buckman 1905) (Spath also listed determinations of these ammonites in Hollingworth & Taylor, 1951 : 14). This fauna dates the Northampton Sand as Opalinum Zone, probably the upper half (Costosum Subzone), so that, as had been originally pointed out by Buckman and reiterated by Richardson (1926 : 141), the disconformity at the junction of the Upper *Leda ovum* Beds and the Northampton Sand represents the top subzone of the Bifrons Zone, the Variabilis, Thouarsense and Levesquei Zones of the Upper Lias, and probably part of the Opalinum Zone at the base of the Inferior Oolite.

There are now no exposures of any part of the Upper Lias of Northamptonshire from which worthwhile ammonite collections can be obtained. The following succession of the Unfossiliferous Beds and the *Leda ovum* Beds is taken from Thompson's descriptions, and includes redeterminations of all the ammonites found in these beds. The succession for the Upper Cephalopod Bed down to the Marlstone Rock Bed is that measured in 1962 and 1963 in the Iron Cross quarry (SP 519547) 1·5 km north of Byfield, and all the ammonites found in similar quarries by Thompson are included in the determinations. It is closely similar to the section recorded by Thompson (1885 : 301–302) near the railway south-west of Byfield (SP 512528).

15. **Northampton Sand.** Sideritic limestones of varying type and composition. *Leioceras* spp., *Bredyia* spp., *Tmetoceras scissum* (Benecke), *Alocolytoceras* sp. and *Pachylytoceras* sp. have been obtained from the upper part of the 'ironstone', i.e. the Main Oolitic Ironstone Group (Hollingworth & Taylor 1951 : 39), 2–3 m above the base, indicating the Opalinum Zone, ? Costosum Subzone (see Hollingworth & Taylor 1951 : 14 for determinations, and Thompson 1927 : 65 and Richardson 1926 : 147, 149 for position within the Northampton Sand).

14. **Nodule Bed.** Layer of grey argillaceous limestone nodules derived from the Upper Lias, of varying sizes and shapes, and worn and stained a variety of colours, set in a matrix of clay or sand, sometimes phosphatic or calcareous. Many fossils in places, especially brachiopods, and sometimes the matrix is composed of crushed shells; none are diagnostic of age which is probably Opalinum Zone; derived *Hildoceras bifrons* (Bruguière) common . . . . 0·08–0·30 m (3 in–1 ft)

Zone of *Hildoceras bifrons*
Subzone of *Peronoceras fibulatum*

13. **Upper *Leda ovum* Beds.** Clay, blue or yellow, sandy and micaceous in places, with much iron pyrites, and nodules of grey argillaceous limestone, sometimes in rows. *Nuclana* ['*Leda*'] *ovum* (J. Sowerby) occurs only in small numbers. *Phymatoceras* cf. *iserense* (Oppel) (Buckman 1898 : xvii; suppl. pl. 2, figs 1, 2), *P.* cf. *narbonense* (Buckman 1898 : xiv; suppl. pl. 2, figs 3, 4), *Porpoceras vortex* (Simpson), *Pseudolioceras lythense* (Young & Bird), *Harpoceras subplanatum* (Oppel), *Hildoceras bifrons*, *Phylloceras heterophyllum* (J. Sowerby), *Lytoceras cornucopia* (Young & Bird) . . . 4·50 m (15 ft)

12. **Oyster Bed.** Continuous row of large grey nodules of argillaceous limestone, white on the outside, bored and often encrusted with oysters and serpulids. Occasional *Hildoceras bifrons* . 0·18 m (7 in)

11. **Middle *Leda ovum* Beds.** Blue clay, with nodules of grey argillaceous limestone. *Nuculana* ['*Leda*'] *ovum* abundant, no gastropods. *Zugodactylites braunianus* (d'Orbigny), *Z. thompsoni* sp. nov., *Peronoceras fibulatum* (J. de C. Sowerby), *P. subarmatum* (Young & Bird), *P. perarmatum* (Young & Bird), *Pseudolioceras lythense* (Young & Bird), *Harpoceras soloniacense* (Lissajous), *H. subplanatum* (Oppel), *Hildoceras bifrons*, *Phylloceras heterophyllum* . . . . 11 m (35 ft)

10. **Lower *Leda ovum* Beds** (or *Cerithium* Beds). Blue clay, with nodules of grey argillaceous limestone. *Nuculana* ['*Leda*'] *ovum* common, *Procerithium* (*Xystrella*) *armatum* (Goldfuss) and other gastropods abundant, and distinguish the beds from the Middle *Leda ovum* Beds. *Zugodactylites braunianus* (d'Orbigny) (Buckman 1926 : pl. 658; 1927 : pl. 720), *Z. rotundiventer* Buckman (1927 : pl. 743), *Z. thompsoni* sp. nov., *Z. pseudobraunianus* (Monestier), *Peronoceras turriculatum* (Simpson), *P. fibulatum*, *P. subarmatum*, *P. perarmatum*, *Pseudolioceras lythense*, *Harpoceras soloniacense* (Buckman 1927 : pls 684, 721, 722), *Hildoceras bifrons*, *Phylloceras heterophyllum* . . . . 11 m (35 ft)

9. Unfossiliferous Beds (part). Blue clay, with a few large nodules of grey argillaceous limestone near the top. *Nuculana ovum* absent. *Peronoceras turriculatum, P. fibulatum, P. subarmatum, P. perarmatum, Harpoceras soloniacense, Hildoceras bifrons* . . . . 4·60 m (15 ft)

Subzone of *Dactylioceras commune*

8. Unfossiliferous Beds (part). Blue clay. *Dactylioceras* cf. *commune* (J. Sowerby) in bottom 3 m, no fossils in top 15 m . . . . 18 m (60 ft)

7. Upper Cephalopod Bed. Limestone, brown, ferruginous, flaggy or rubbly, and shaly in places. Ammonites abundant: *Dactylioceras commune* (Thompson 1886 : 26; pl. 1, figs 3a, 3b, 4; Buckman 1926 : pl. 657), *D. praepositum* (Buckman), *Nodicoeloceras* sp. indet., *Hildoceras sublevisoni* Fucini, *Harpoceras falciferum* (J. Sowerby), *Pseudolioceras lythense, Frechiella subcarinata* (Young & Bird) (Arkell 1951 : pl. 1, fig. 3), *Lytoceras metorchion* (Buckman 1926 : pls 666, 681), *Phylloceras heterophyllum* . . . . 0·38 m (1 ft 3 in)

6. Clay, grey or brown, marly, sandy or ferruginous in patches, with small white limestone nodules. Ammonites small and poorly preserved, but *Dactylioceras commune, Hildoceras sublevisoni* and *Harpoceras falciferum* are common . . . . 0·9 m (3 ft)

Zone and Subzone of *Harpoceras falciferum*

5. Lower Cephalopod Bed. Limestone, hard, pale yellow-brown, blue interior, sometimes sandy, oolitic or shaly, and in three thin layers in places. Ammonites only occasional, but microconchs and large macroconchs of *Harpoceras falciferum* occur (Thompson 1885 : 309, fig. 1), also *Dactylioceras* sp. indet., *Nodicoeloceras crassoides* (Simpson) (Thompson 1885 : 309, fig. 2), and *Ovaticeras ovatum* (Young & Bird) (see below) . . . . 0·23 m (9 in)

4. Clay, blue-grey and brown, marly, with a few small white limestone nodules. Ammonites rare. *Dactylioceras* sp. indet. . . . . 0·9 m (3 ft)

Subzone of *Harpoceras exaratum*

3. Abnormal Fish Bed. Limestone, hard, pale blue-grey, brown when weathered, containing large grey ooliths in places. Separated from the bed below by a parting in most places. Full of tiny black fish fragments, including some whole teeth, and occasional pieces of wood. Well-preserved ammonites abundant. *Harpoceras exaratum* (Young & Bird), *H. elegans* (J. Sowerby), *H. serpentinum* (Schlotheim), *Hildaites murleyi* (Moxon) (Buckman 1928 : pl. 772), *Dactylioceras* (*Orthodactylites*) *semiannulatum* sp. nov., *Dactylioceras* sp. indet., *Nodicoeloceras crassoides* (Simpson), *Lytoceras crenatum* (Buckman) (Thompson 1885 : 200, fig. 6; Buckman 1926 : pls 665, 680), *Phylloceras heterophyllum* . 0·15 m (6 in)

Zone of *Dactylioceras tenuicostatum*
Subzone of *Dactylioceras semicelatum*

2. Transition Bed. Limestone, pale brown, oolitic, ferruginous. Welded to the top of the Marlstone Rock Bed. *Tiltoniceras antiquum* (Wright), *Dactylioceras* (*Orthodactylites*) *directum* (Buckman), *D.* (*O.*) *semicelatum* (Simpson) . . . . 0·05 m (2 in)

Subzones of *Dactylioceras tenuicostatum, D. clevelandicum and Protogrammoceras paltum,*
and Zone of *Pleuroceras spinatum*

1. Marlstone Rock Bed. Limestone, green, red-brown when weathered, full of chamosite ooliths. *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (Young & Bird) rare in top 0·15 m; *Pleuroceras spinatum* (Bruguière) occurs rarely below the top 1 m. *Tetrarhynchia tetrahedra* (J. Sowerby) and *Lobothyris punctata* (J. Sowerby) abundant below the top 1 m. Thickness at Byfield . . . 2·1 m (7 ft)

The *Ovaticeras ovatum* recorded in the Lower Cephalopod Bed is BM C.79469 (Miss A. E. Baker Collection), a single specimen that came from Gayton, 8 km SW of Northampton. It is a typical example of *Ovaticeras*, 100 mm in diameter, and is the only specimen known from outside Yorkshire and Lincolnshire. Its horizon was not recorded, but the matrix is that of the Lower Cephalopod Bed, which agrees with the Falciferum Subzone age of the species in Yorkshire.

In a small area around the villages of Milton and Bugbrooke, 5–8 km SW of Northampton, the condensed Abnormal Fish Bed (bed 3) expands to form two or three limestones separated by shales. The maximum development is at Milton where the following succession was recorded by Thompson (1892 : 336). It was seen again in 1958 below a motorway bridge at SP 735567.

Bed 3, total thickness 0·67 m (2 ft 2 in):

3f. Inconstant Cephalopod Bed. Limestone, pale brown-grey, fine-grained, slightly oolitic in places. Large specimens of *Harpoceras serpentinum* common, also *H. elegans*, *Hildaites murleyi*, *Dactylioceras* sp. indet. and *Lytoceras* sp. indet.	0·10 m (4 in)
3e. Shale, grey-brown, marly. Only slightly softer than the Inconstant Cephalopod Bed. Large crushed *Harpoceras serpentinum*	0·10 m (4 in)
3d. Fish Bed. Brown, crystalline, nodular limestone, oolitic in places, containing small fish fragments. *Harpoceras exaratum*, *Hildaites murleyi*	0·05 m (2 in)
3c. Shale, pale brown, finely laminated ('paper' shale). *Harpoceras exaratum*	0·10 m (4 in)
3b. Fish Bed. Brown crystalline limestone, oolitic in places, in large slabs forming a continuous bed, containing small fish fragments. *Harpoceras exaratum*, *Hildaites murleyi*	0·05 m (2 in)
3a. Shale, finely divided at top, passing down into clay with red sandy layers	0·27 m (10 in)
2. Transition Bed. Limestone, marly and oolitic. *Tiltoniceras antiquum*, *Dactylioceras* (*Orthodactylites*) *directum*	0·15 m (6 in)

At Bugbrooke, 6·5 km west of Milton, the thickness of bed 3 has diminished to 0·43 m (1 ft 5 in) and only one Fish Bed is present. The following succession was seen in an excavation made by Thompson (1892 : 337; 1910 : 463–464).

3f. Inconstant Cephalopod Bed. Hard limestone. Large specimens of *Harpoceras serpentinum*	0·20 m (8 in)
3e. Shale, finely laminated. Crushed *H. serpentinum*	0·10 m (4 in)
3b–d. Fish Bed. Limestone in large slabs. *H. exaratum*, *Hildaites murleyi*, *Lytoceras crenatum*	0·05 m (2 in)
3a. Shale, finely laminated	0·08 m (3 in)

The examples of *Hildaites murleyi* in the Fish Bed were recorded by Thompson as *Ammonites latescens* Simpson, and later (Thompson 1910 : 462, 463) the term 'Fish Bed, or Latescens Zone' was used. When the holotype of *A. latescens* was figured by Buckman (1913 : pl. 79) it was shown to be a species of *Pseudogrammoceras* from the Thouarsense Zone of Yorkshire.

Thompson's collection also contains specimens of *Harpoceras elegans* and *H. serpentinum* marked 'Inconstant Cephalopod Bed' from quarries at nearby localities at Rothersthorpe, Weedon and Harpole. Finally, in a railway cutting near Watford, about 10 km NW of this area, Thompson (1885 : 191–193) recorded a variable sequence of beds that appears to show a transition between the Inconstant Cephalopod Bed – Fish Bed succession and the Abnormal Fish Bed. In one part of the cutting the Abnormal Fish Bed, Transition Bed and Marlstone Rock Bed form one block of stone, in another part the Abnormal Fish Bed is separated from the Transition Bed by a thin bed of shale or clay, while the thickest development in the cutting consists of the Inconstant Cephalopod Bed (0·15 m), separated by shale (0·06 m) from the Fish Bed (0·08 m), and the latter separated by sandy clay (0·06 m) from the Transition Bed.

At all localities further west and south-west from Welton (Thompson 1886 : 19), Daventry, Staverton and Catesby southwards to Chipping Warden, bed 3 is condensed into the Abnormal Fish Bed and is the same as already described at Iron Cross quarry, Byfield. The only succession which does not conform is one described by Thompson (1896*a* : 426) from excavations for bridge foundations at SP 542534, 0·8 km north of Woodford Halse. Thompson saw a bed which he interpreted as the Inconstant Cephalopod Bed only 0·05 m above the Fish Bed, but which 'often merges into the Fish Bed below'. It contained large ammonites recorded by Thompson as *A. strangewaysi*, which are either *Harpoceras serpentinum* or *H. falciferum*, but more interesting were the two large specimens figured by Buckman (1926 : pls 666, 681) as the holotypes of *Orcholytoceras metorchion* and *O. appropinquans*, which are both now interpreted as *Lytoceras metorchion*. They have a distinctive type of preservation in which parts of the whorls are distorted or broken and displaced, and the matrix does not differ from that of the Lower and Upper Cephalopod Beds. Specimens of *Lytoceras* with this characteristic preservation have been found by other collectors, including the author at Iron Cross quarry, Byfield, only in the Upper Cephalopod Bed, and some doubt must be thrown on Thompson's observations, and on the presence of the Inconstant Cephalopod Bed at Woodford Halse. If present at Woodford Halse, it would be 15 km west of the Milton–Bugbrooke area and would be the only occurrence of the bed outside that area.

The Yorkshire coast

In all previous descriptions of stratigraphically localized collections of ammonites from the Upper Lias of the Yorkshire coast it has been stated that species of *Zugodactylites* do not occur in Yorkshire (Buckman 1915*a* : 102; Dean 1954 : 171; Howarth 1962*b* : 415). So the chance discovery of a complete and beautifully preserved example of *Zugodactylites braunianus* at Whitby in 1968 was surprising enough. More interesting was its horizon in bed 63, at about the middle of the Fibulatum Subzone as then defined (Howarth 1962*b* : 397), and this agreed with the conclusion arrived at from study of the Northamptonshire ammonites, that *Zugodactylites* occurred wholly within the stratigraphical range of *Peronoceras*. Confirmation of this distribution was then sought in Yorkshire: in 1973 a few more *Zugodactylites* were found in beds 62–64 of the main outcrop at Whitby, and the total number known is now six, including the small fragment recorded previously (Howarth 1962*b* : 397, bed 64) as *Peronoceras* cf. *turriculatum*. This compares with 106 specimens of *Peronoceras* collected from beds 60–63, so although *Zugodactylites* is much less common than *Peronoceras* at Whitby, it can be shown to occur in the lower part of the Fibulatum Subzone. At the same time a larger collection of *Zugodactylites* was made from bed xxxi (Howarth 1962*b*: 401) on the foreshore below Ravenscar: 18 specimens are now known, including a poorly preserved *Z. braunianus* recorded previously as *Peronoceras* sp. indet. (BM C.68504), and an excellent *Z. thompsoni* sp. nov. (Pl. 8, fig. 2) recorded previously as *Peronoceras* aff. *subarmatum*. *Peronoceras* occurs only in beds xxix and xxx below and does not accompany these *Zugodactylites*, and this probably represents merely a local variation in their distribution when compared with Whitby. As explained later (p. 245), now that the Braunianus Subzone has to be abandoned, the Fibulatum Subzone is extended upwards in Yorkshire, up to the base of the Crassum Subzone in bed 72 at Whitby and in bed xiv at Ravenscar.

The following is a record of the new ammonites collected in Yorkshire, and includes all the specimens of *Zugodactylites* that are now known (all specimens BM).

1. **Long Bight to Rail Hole Bight,** foreshore east of Whitby (see Howarth 1962*b* : 397; pl. 28).
   Bed 64. *Zugodactylites braunianus* (C.68344) 0·30 m above the base.
   Bed 63, row of scattered doggers at top. *Z. braunianus* C.78218–9; *Peronoceras fibulatum* C.78206–14; *P. turriculatum* C.78215–7.
   Bed. 63, row of doggers 0·30 m below top. *Zugodactylites braunianus* C.78204–5; *Peronoceras turriculatum* C.78198–200; *Hildoceras bifrons* C.78203; *Pseudolioceras lythense* C.78201–2.
   Bed 63, lower half. *Peronoceras fibulatum* C.78178–91; *P. perarmatum* C.78194–7; *Phylloceras herophyllum* C.78192.
   Bed 62. *Zugodactylites braunianus* C.78193; *Peronoceras fibulatum* C.78175–7.
2. **Foreshore below Ravenscar** (see Howarth 1962*b* : 401; pl. 27).
   Bed xliii. *Porpoceras vortex* C.78251–2; *P. verticosum* C.78229–31.
   Bed xlii. *Harpoceras subplanatum* (Oppel) C.75830.
   Bed xxxii. *Hildoceras bifrons* C.78248.
   Bed xxxi. *Zugodactylites braunianus* C.68504, C.78232–47; *Z. thompsoni* C.68503; *Pseudolioceras lythense* C.78249–50.
   Bed xxx. *Peronoceras fibulatum* C.78224–8; *P. perarmatum* C.78253; *Pseudolioceras lythense* C.78254; *Phylloceras heterophyllum* C.78255.

Critical re-examination of the Whitby ammonites also shows that the rich *Porpoceras* fauna in beds xliii and xlii at Ravenscar is also found as poorly preserved ammonites in the basal 1·5 m (5 ft) of bed 72 at Whitby (Howarth 1962*b* : 396). C.68525–6 are two medium-sized fragments of *P.* cf. *vortex* that have alternating fibulate-tuberculate and simple ribs, C.68527 is a small ammonite, apparently complete at 35 mm diameter and possible adult, that is probably a *Porpoceras*, while C.68528 is a fragment showing the typical ornament of *P. verticosum*. The lowest *Catacoeloceras crassum* occur in considerable numbers 1 m (3 ft) higher up, i.e. 1·5 m (5 ft) below the top of bed 72. So beds xliii and xlii at Ravenscar are to be correlated with the lowest 1·5 m of bed 72 at Whitby.

Zonal subdivisions and correlation with Yorkshire

The sequence of ammonite faunas in the Northamptonshire Upper Lias is closely similar to the sequence on the Yorkshire coast (Howarth 1962*b* : 1973), and much of the standard succession of zones and subzones for the basal half of the Upper Lias in north-west Europe is based on these two areas (Dean, Donovan & Howarth 1961). The zonal divisions and a comparison between Yorkshire and Northamptonshire are given in Table 1.

Table 1. Zone and subzone divisions and correlation between Northamptonshire and Yorkshire. The bed numbering for Yorkshire is from Howarth 1962*b* for the Upper Lias, and from Howarth 1955 : 156 for the Middle Lias.

Zone	Subzone	Northamptonshire	Yorkshire
Hildoceras bifrons	*Catacoeloceras crassum*	(absent)	Bed 72 (upper 2·5 m), xlv–lvi (Cement Shales)
	Peronoceras fibulatum	Upper *Leda ovum* Beds Oyster Bed Middle *Leda ovum* Beds Lower *Leda ovum* Beds Unfossiliferous Beds, top 4·6 m	72 (lower 1·5 m), 60–71, xxix–xliii, ? xliv (Cement Shales and Main Alum Shales)
	Dactylioceras commune	Unfossiliferous Beds, bottom 18 m Upper Cephalopod Bed Bed 6	49–59, xvi–xxviii (Main Alum Shales and Hard Shales)
Harpoceras falciferum	*Harpoceras falciferum*	Lower Cephalopod Bed Bed 4	48 (Ovatum Band) 41–47(Bituminous Shales)
	Harpoceras exaratum	Inconstant Cephalopod Bed Fish Beds (Abnormal Fish Bed)	35–40 (Jet Rock)
		(bottom of subzone absent)	33, 34 (Jet Rock)
Dactylioceras tenuicostatum	*Dactylioceras semicelatum*	Transition Bed	28–32 (Grey Shales)
	Dactylioceras tenuicostatum	Marlstone Rock Bed, top ? 1 m	20–27 (Grey Shales)
	Dactylioceras clevelandicum		18, 19 (Grey Shales)
	Protogrammoceras paltum		1–17 (Grey Shales) 26–28 (Ironstone Series)
Pleuroceras spinatum	*Pleuroceras hawskerense*	Marlstone Rock Bed, below top ? 1 m	20–25 (Ironstone Series)
	Pleuroceras apyrenum		5–19 (Ironstone Series)

Species of *Pleuroceras*, characteristic of the Middle Lias Spinatum Zone, are only rarely found in the Marlstone Rock Bed, and always occur below the top 1 m. The junction between the Middle and Upper Lias occurs about 1 m below the top of the Marlstone Rock Bed, but its exact position is unknown owing to the rarity of ammonites, and there is no lithological break within the ironstone. The lowest two subzones of the Tenuicostatum Zone are not represented by ammonites, but the Tenuicostatum Subzone is represented by a few examples of the index species in the top 0·15 m of the ironstone. Ammonites first become abundant in the Northamptonshire Upper Lias in the Transition Bed with the appearance of *Dactylioceras semicelatum*, *D. directum* and *Tiltoniceras antiquum*. This is the characteristic fauna of the Semicelatum Subzone and correlates with the top beds of the Grey Shales in Yorkshire. There is little or no palaeontological break between the top of the Marlstone Rock Bed and the Transition Bed.

The Abnormal Fish Bed in western Northamptonshire and the Fish Beds and Inconstant Cephalopod Bed near Northampton belong to the upper two-thirds of the Exaratum Subzone of the Falciferum Zone. *Eleganticeras*, which is characteristic of the lower third of the subzone, is absent in Northamptonshire, and this interval is probably the extent of the disconformity between the Transition Bed and the Abnormal Fish Bed. *Eleganticeras* is a close phylogenetic successor of *Tiltoniceras*, so it is less likely that sedimentation was complete, but *Eleganticeras* absent, in Northamptonshire. The abundant ammonites in the Abnormal Fish Bed are the same as those in beds 35–40 of the Yorkshire Jet Rock, but owing to the condensation *Harpoceras exaratum* and *H. elegans* are mixed together. In addition, the bed contains many well-preserved specimens of *H. serpentinum* and *Hildaites murleyi*, two species that are rare in Yorkshire.

In the more expanded sequence near Northampton, *Harpoceras exaratum* occurs in the Fish Beds, while *H. elegans* occurs in the Inconstant Cephalopod Bed, and this is the same as the relative position of the two species in Yorkshire. *Harpoceras serpentinum* appears to be confined to the Inconstant Cephalopod Bed and the shale immediately overlying the Fish Beds, and with *H. elegans* characterizes the top third of the Exaratum Subzone.

The Lower Cephalopod Bed and bed 4 belong to the Falciferum Subzone. Both contain *H. falciferum* and a single specimen of *Ovaticeras ovatum* has been found in the Lower Cephalopod Bed, and they are to be correlated with the Bituminous Shales and the Ovatum Band in Yorkshire. The base of the Commune Subzone of the Bifrons Zone is marked by the incoming of *Dactylioceras commune* and *Hildoceras sublevisoni* in the clays of bed 6. These two species are abundant and better preserved in the Upper Cephalopod Bed, where *D. praepositum* and *Frechiella subcarinata* also occur. This fauna is the same as in the type area of the Commune Subzone, i.e. the Hard Shales and lower part of the Alum Shales in Yorkshire. *H. falciferum* persists in considerable numbers in the Commune Subzone in Northamptonshire, unlike Yorkshire where it dies out before the top of the Falciferum Subzone. *D. commune* also occurs in the basal 3 m of the Unfossiliferous Beds.

The base of the Fibulatum Subzone is drawn at the first appearance of species of *Peronoceras*, 4·6 m below the top of the Unfossiliferous Beds. Species of *Peronoceras* are more abundant throughout the Lower and Middle *Leda ovum* Beds, where they are accompanied by rich faunas of *Zugodactylites*. It was this apparent sequence of *Peronoceras* in the Unfossiliferous Beds followed by *Zugodactylites* in the *Leda ovum* Beds that led to the original proposal of the Fibulatum and Braunianus Subzones by Buckman (1910*a* : 86). Buckman determined the ammonites, but all the stratigraphical details and ammonite collections had been supplied by Thompson, who published the same sequence shortly afterwards (Thompson 1910 : 461, 462). However, in the same paper, as well as much earlier, Thompson (1910 : 465; 1888 : 83) was aware that *Peronoceras* and *Zugodactylites* occurred together in abundance in the *Leda ovum* Beds. In fact in Northamptonshire it appears that the stratigraphical range of *Zugodactylites* occurs wholly within the range of *Peronoceras*, and the new evidence from Yorkshire confirms the substantial coexistence of the two genera. So the Braunianus Subzone has to be abandoned. A similar conclusion was reached by Guex (1970*b* : 623) on the basis of the position of *Zugodactylites* in the succession at Aveyron, south-east France, though the evidence there is not strong, because *Peronoceras* does not occur (or is very rare) in that area, and the position of *Zugodactylites* can only be compared with that of species of *Hildoceras*.

It is now proposed to retain the Fibulatum Subzone for those beds above the Commune Subzone whose base is marked by the first appearance of *Peronoceras*. This subzone will be extended up to include beds that contain the closely related genus *Porpoceras*, i.e. the Upper *Leda ovum* Beds in Northamptonshire, and beds xliii and xlii at Ravenscar in Yorkshire. This is the top of the Lias in Northamptonshire: if the top 1–2 m of the Upper *Leda ovum* Beds belong to the top subzone of the Bifrons Zone (as in Leicestershire, see below), then the diagnostic ammonites of the genus *Catacoeloceras* are not present. These conclusions are not contradicted by the presence of *Phymatoceras* in the Upper *Leda ovum* Beds, a genus that is usually held to be typical of the Variabilis Zone in Britain. In France, *Phymatoceras* first appears immediately below the main *Porpoceras* horizon (Guex 1972 : 619), and mid-Bifrons Zone *Phymatoceras* also occur in Italy (Pinna & Levi-Setti 1973), though with less accurately documented stratigraphical position. The Northamptonshire specimens are not out of place in the Fibulatum Subzone, therefore, and this is the lowest occurrence of the genus in Britain. *Harpoceras* is present in considerable numbers in the Northamptonshire Fibulatum Subzone: *H. soloniacense* occurs in the Unfossiliferous and Lower and Middle *Leda ovum* Beds, and is the phylogenetic successor of *H. falciferum* of the Commune Subzone; the more involute *H. subplanatum* (Oppel) occurs in the Middle and Upper *Leda ovum* Beds. The latter species is the highest occurrence of *Harpoceras* in Britain, after which the genus became extinct. In Yorkshire, *Harpoceras* disappeared much earlier, at about the middle of the Falciferum Subzone, but a single large specimen of *H. subplanatum* (BM C.75830) has been found in bed xlii at Ravenscar (the *Porpoceras* horizon) since the succession was described previously (Howarth 1962*b*).

A new index ammonite is required for the top subzone of the Bifrons Zone. The best choice is *Catacoeloceras crassum* (Young & Bird), which was first used as a zonal index by Corroy & Gérard (1933) in south-east France (see Dean, Donovan & Howarth 1961 : 482–483). It is abundant in the upper half of the Cement Shales in Yorkshire, and first appears not far above the *Porpoceras* horizon (Howarth 1962*b* : 396, 400, 402). The upper limit of the subzone, and of the Bifrons Zone, is marked by the first appearance of *Haugia* at the base of the Variabilis Zone. *Catacoeloceras crassum*, other species such as *C. dumortieri* Maubeuge, and species of *Collina* form a distinct group of ammonites, easily distinguished from *Peronoceras* and *Porpoceras* of the Fibulatum Subzone.

Correlations with other areas

England

The *Leda ovum* Beds used to be well exposed in Northamptonshire as far north as the Kettering – Corby – Thrapston area, and they could still be seen recently in the bottom of a gravel pit near Thrapston, where the uppermost beds yielded *Hildoceras bifrons*, indicating the Fibulatum Subzone. Ammonites obtained from former exposures in the north-east of the county and in Leicestershire and Rutland as listed by Woodward (1893 : 280–284) cannot now be checked, except for a typical *H. bifrons* from Helpston, north-west of Peterborough, which again indicates the Fibulatum Subzone. There is, however, a good example of *Catacoeloceras crassum* (Young & Bird) in the collections of the Institute of Geological Sciences (GSM 22519) whose locality is merely recorded as 'Leicestershire'. It is preserved in typical *Leda ovum* Beds grey clay matrix with a white chalky shell, and must indicate that the clays in the area from which it came extend up into the base of the Crassum Subzone. It compares closely (Pl. 8, fig. 6) with many of the specimens of *C. crassum* from the Cement Shales at Ravenscar, Yorkshire. It was presented to the Geological Survey before 1865 by Lady Exeter (of Burghley House, Stamford), and the most likely locality from which it could have come is the top of the Lias beneath the Northampton Sand that caps the hill at Nevill Holt (SP 815935), near Medbourne, south-east Leicestershire. This is only 10–13 km north of the Kettering – Corby exposures, and details of some of the former exposures in the area were given by Judd (1875 : 82; the *Amm. crassus* Phillips recorded by Judd was apparently a determination given to ammonites low in the Upper Lias clays and from the Commune Subzone, and it is unlikely to refer to the true *Catacoeloceras* of the Crassum Subzone). A less likely area for the specimen is the Buckminster – Sproxton – Croxton Kerrial area of north-east Leicestershire where the junction between the Lias and the Northampton Sand also occurs.

The is no evidence for the presence of the Crassum Subzone anywhere else, for near Grantham nine specimens of *Porpoceras vortex* and *P. verticosum* have been obtained from the top part of the Bifrons Zone clays, some only 1–2 m below the top of the Lias, others perhaps 6 m below (see p. 280). These show that the top of the Lias at Grantham is near or at the top of the Fibulatum Subzone. They are accompanied by specimens of *Hildoceras bifrons* and *Pseudolioceras lythense*. At Lincoln the Lias was formerly exposed in two brickpits described by Ussher (1888 : 33–35) and Trueman (1918 : 103–107). The Bifrons Zone clays are about 15 m thick and have yielded many ammonites (mainly British Museum (Natural History) collections) preserved as pyritic or septarian nodules. There are many *Dactylioceras commune*, including variants with thick and massive whorls, and some *Hildoceras sublevisoni*, of the Commune Subzone. Also there are large well-preserved examples of *H. bifrons*, several *Peronoceras fibulatum*, *P. subarmatum* and *P. perarmatum*, and a single very large (110 mm diameter) and coarsely ribbed *Porpoceras vortex* (BM C.19857), all from the Fibulatum Subzone, and the last species from near the top of that subzone. Throughout Northamptonshire, and at Grantham and Lincoln, the ammonities show that the highest beds of the Lias beneath the Northampton Sand ironstone belong to the top of the Fibulatum Subzone, because the diagnostic genus *Porpoceras* is known from each area. Only at one poorly-defined area of eastern Leicestershire is there any evidence for the overlying Crassum Subzone, and the single known *C. crassum* requires the presence of only an extra 1 m or thereabouts of beds at the base of that subzone. So the top of the Lias maintains an almost constant horizon between Northamptonshire and Lincoln, and there is disconformity, but no regional or angular unconformity, between it and the Northampton Sand. Trueman's (1918 : 110, fig. 5) diagram (redrawn by Arkell 1933 : 177, fig. 31), which shows a substantial angular unconformity resulting in the overstep of the Lias by the Northampton Sand between Northampton and Lincoln, is not correct. It was based on wrong age determinations of the Dactylioceratidae. The Bifrons Zone clays disappear quickly north of Lincoln and are not are seen again until the Yorkshire basin north of Market Weighton.

South-westwards from Northamptonshire the clays of the Bifrons Zone extend into Oxfordshire and steadily diminish in thickness. The ammonites from the Hook Norton railway cuttings listed by Woodward (1893 : 268–269) can be seen in many collections, and include many well-preserved *Peronoceras fibulatum* and other species. No new information has been obtained about the exposures farther south in Gloucestershire, Somerset or Dorset.

Southern France, the Alps and Italy

The succession of Dactylioceratidae in the Bifrons Zone at Aveyron, southern France, worked out in detail by Guex (1972), is closely similar to that of Northamptonshire and Yorkshire, though a major difference is the rarity of the genus *Peronoceras* at Aveyron. The Commune Subzone is represented in horizons I and II (see Table 2) of Guex (1972 : 618) which contain *Dactylioceras* cf. *commune* and *Hildoceras sublevisoni*. In horizon III the latter species is replaced by the first *H. bifrons*, and *Peronoceras* is probably represented by small inner whorls of *P. turriculatum* (Simpson) (Guex 1972 : pl. 8, figs 5, 7–9). This is the lowest fauna of the Fibulatum Subzone. Rich faunas of *Zugodactylites* appear in horizon IV. It was this close appearance of *Z. braunianus* above the first *H. bifrons* (which marks the base of the Bifrons Subzone (=Fibulatum Subzone) in France), that led Guex (1970*b*) to reject the use of *Z. braunianus* as an index species for a subzone above the Bifrons (=Fibulatum) Subzone. Guex inferred that *Zugodactylites* must occur in the Bifrons Subzone, though he did not recognize *Peronoceras* at Aveyron, and so he could not work out the relative distribution of the two genera. The coincidence of the ranges of *Peronoceras* and *Zugodactylites* has now been demonstrated in England, so it is possible to correlate horizons III and IV at Aveyron with the lower part of the Fibulatum Subzone. *Porpoceras vortex* appears in abundance in horizon VII, which correlates with the English *Porpoceras* horizon, then other species of *Porpoceras* occur higher up in horizon IX and in the lower part of horizon X. Thus, horizons III–lower X are equivalent to the Fibulatum Subzone. As in Northamptonshire *Harpoceras soloniacense* and *H. subplanatum* occur throughout this subzone at Aveyron, and the first *Phymatoceras* appear about the middle of the subzone (horizon VI). The base of the Crassum Subzone is marked by the incoming of *Catacoeloceras* in the upper part of horizon X, and it appears in abundance in horizon XI. *Catacoeloceras* remains an abundant ammonite at Aveyron up to the top of the Crassum Subzone (horizon XIII) and throughout the Variabilis Zone (horizons XIV–XVIII), and it is accompanied by many other Dactylioceratidae, mainly belonging to the genus *Collina*, that are rare in England. *Harpoceras* became extinct at the top of the Fibulatum Subzone, and does not occur in the Crassum Subzone at Aveyron. Table 2 gives a summary of the horizons and the main diagnostic ammonites at Aveyron, and their English subzonal equivalents. At the left of the table are the different subzonal divisions used at Aveyron (after Gabilly *et al.* 1971), which are based on the succession of species of *Hildoceras*, and they are exactly equivalent to the three English subzones. The same sequence of *Hildoceras* species occurs in England, but it would be very difficult to apply subzones based on them to the English succession, especially in the upper two subzones, because *Hildoceras* is less common in England, and the species are much more alike and more difficult to identify than the Dactylioceratidae that accompany them. In particular *H. bifrons* and *H. semipolitum* are merging or overlapping species. They are distinct when fully developed, but confusing when the considerably variable *H. bifrons* is slowly evolving into the equally variable *H. semipolitum*. This is also the case at Aveyron, where the population of *Hildoceras* in horizon VIII already contains specimens determined as *H. semipolitum* as well as *H. bifrons*, and other forms intermediate between the two, yet Guex does not draw the base of the Semipolitum Subzone until the middle of horizon X. On the other hand, the population in horizon XII still contains specimens determined as *H. bifrons* as well as *H. semipolitum*. Either the ranges of the two species overlap a great deal, or there is really only one slowly evolving species. Undoubtedly subzones based on Dactylioceratidae could be applied to the Aveyron succession within the Bifrons Zone, and they would be more distinctive, more precise and easier to use. In fact it appears that the boundary between the Bifrons and Semipolitum Subzones was placed by Guex in a position that accorded with a change in the Dactylioceratidae, rather than a change in the two species of *Hildoceras* that he used as subzonal indexes.

Table 2. Ammonite faunas and subdivisions of the Bifrons and Variabilis Zones at Aveyron, and the equivalent English subzones.

Divisions at Aveyron	Horizons	Main ammonites	English equivalents
Variabilis Zone	XVIII	*Haugia* spp. *Catacoeloceras* spp.	Variabilis Zone
	XVII		
	XVI		
	XV		
	XIV		
Hildoceras semipolitum Subzone	XIII	*Catacoeloceras*, *Hildoceras semipolitum*, *H. bifrons*	*Catacoeloceras crassum* Subzone
	XII		
	XI		
	upper X		
Hildoceras bifrons Subzone	lower X	*Porpoceras* spp., *Harpoceras*, *Hildoceras bifrons* and spp.	*Peronoceras fibulatum* Subzone
	IX		
	VIII		
	VII		
	VI	*H. bifrons*, *Harpoceras*	
	V		
	IV	*Zugodactylites*, *H. bifrons*	
	III	*H. bifrons*, *Peronoceras*	
Hildoceras sublevisoni Subzone	II	*Hildoceras sublevisoni* *Dactylioceras* sp.	*Dactylioceras commune* Subzone
	I		

In Austria and Italy the succession of ammonites in the Bifrons Zones appears to be largely in accordance with the English and French successions. The faunas at Kammerker, Austria, have been described by Fischer (1966) and those in Italy by Pinna & Levi-Setti (1971). There are many discrepancies in the determination of individual ammonites that could not be sorted out without examination of the whole collections, and the stratigraphical relationships of the Italian forms is not known in sufficient detail for bed-by-bed comparisons to be made with England. It is to be noted, however, that *Porpoceras* and *Catacoeloceras* are abundant in some parts of Italy in the equivalent of the upper part of the Bifrons Zone and in the Variabilis Zone, but the presence of *Peronoceras* and *Zugodactylites* is more problematical.

North-eastern Siberia, northern Alaska, arctic Canada, Greenland, Spitzbergen

The new evidence for the zonal ranges for the Northamptonshire Bifrons Zone Dactylioceratidae has considerable bearing on the dating of the *Zugodactylites*, *Porpoceras* and *Pseudolioceras* faunas that are widespread over a very large area from north-eastern Siberia eastwards to Spitzbergen. The succession in Siberia has been described in detail by Dagis (1968 : 70–98; 1974 : 65–79) and that in Canada, Greenland and Spitzbergen by Frebold (1975 : 18–21, table 1), who summarized all previous work. Throughout much of this vast area the Commune Subzone is represented by *Dactylioceras commune*, accompanied by other species in Siberia. The next higher fauna consists of *Zugodactylites braunianus* and other species, which are abundant in Siberia (Dagis 1968 : 39–56) and closely comparable with those in Northamptonshire, and less common but still characteristic *Zugodactylites* in the Canadian Arctic. Hitherto this fauna has been placed at the top of the Bifrons Zone in the 'Braunianus Subzone', with a gap below representing the missing Fibulatum Subzone. However, it is now clear that this is a Fibulatum Subzone fauna, and there is no need for a gap between it and the underlying Commune Subzone.

The next higher fauna consists of species of *Porpoceras* and *Pseudolioceras*. It occurs over the whole area, has been referred to as a widespread Arctic marker bed, and contains *Porpoceras polare* (Frebold), *P. spinatum* (Frebold), *Pseudolioceras* cf. *compactile* (Simpson) and other species of *Pseudolioceras*. In Siberia *Porpoceras polare* follows closely above the *Zugodactylites* fauna, then *Pseudolioceras rosenkrantzi* Dagis occurs higher up (Dagis 1968 : 76). A summary of all the occurrences and the reasons for correlating the bed with the Thouarsense Zone, Striatulum Subzone, in Europe, was given by Frebold (1975 : 19–20). This correlation relies entirely on the dating of *Pseudolioceras compactile* (Simpson) in Europe. Species of *Pseudolioceras* are poor age indicators, however, for they are very difficult to determine, even with large European collections of known stratigraphy, in which single-horizon collections show considerable variation. On the other hand, the two Arctic species of *Porpoceras*, though not known in Europe, are definitely species of *Porpoceras*, showing the characteristic mixture of fibulate and single ribs at larger sizes. All the evidence from Northamptonshire, Yorkshire, south-east France and Italy shows that *Porpoceras* occurs in what is now called the Fibulatum Subzone, before the incoming of *Catacoeloceras* of the Crassum Subzone. *Porpoceras* disappears with the advent of *Catacoeloceras*. Therefore, a better correlation of the Arctic *Porpoceras – Pseudolioceras* bed is with the top of the Fibulatum Subzone in Europe. All the specimens of *Pseudolioceras* in that bed could be accommodated in, or are closely allied to, *P. lythense* (Young & Bird), a highly variable species that occurs in the Bifrons Zone of western Europe, so there is no need to postulate a younger age for the Arctic bed because of the *Pseudolioceras* fauna that it contains. This correlation does not necessarily apply to the higher horizon in Siberia (i.e. bed 11 of Dagis 1968 : 76–77), where *Porpoceras* is absent and *Pseudolioceras rosenkrantzi* occurs, which may belong to a higher zone.

Palaeontology

Family **DACTYLIOCERATIDAE** Hyatt 1867

Many studies of Dactylioceratidae have been made in recent years since the stratigraphical sequence of most of the Yorkshire coast Upper Liassic species was worked out in an earlier paper (Howarth 1962*b*). The main descriptions are by Dagis (1968), Fischer (1966), Géczy (1966), Guex (1971, 1972, 1973*a*, 1973*b*, 1974), Howarth (1973), Pinna & Levi-Setti (1971), Sapunov (1963) and Schmidt-Effing (1972). Stratigraphical knowledge of the relationships between the forms described was very variable, and in cases where it was, of necessity, poor in detail, as in the Italian faunas described by Pinna & Levi-Setti (1971), then a classification based mainly on morphological divisions had to be adopted. Where the stratigraphy was better known, it has been used as a guide to the generic and specific divisions to varying degrees, and many conflicting opinions have been expressed.

When a single-bed collection of Dactylioceratidae is obtained, one of the most striking features often seen is the wide variation, usually in whorl breadth, rib-density and amount of tuberculation. In this respect they are often many times more variable than the Hildoceratidae that accompany them in equal abundance at many localities. Three different methods can be used for classification of such a collection – (1) reference to a single variable species, (2) division into two or more species or (3) division into two genera and several species. Method (3) is inevitable with small collections of indifferently preserved specimens, or where the stratigraphy is not accurately known. However, where collections are larger, better preserved and include adults, and where the stratigraphy is accurately known, then the variation at a single horizon is often seen to be continuous, and any specific or generic divisions are arbitrary divisions of that variation. A factor of more significance is that when enough single-bed collections from several zones have been examined, it becomes apparent that diagnostic characters are often held in common by all the specimens from a single bed, regardless of their wide variation in other characters. For example, in the collections from the Tenuicostatum Zone Grey Shales of Yorkshire (Howarth 1973) all the specimens at each horizon possess the mixture of single and bifurcating ribs at some growth stage that is characteristic of the subgenus *Orthodactylites*, regardless of whether the whorls are compressed or broad, the ribbing dense or sparse, or tubercles present or absent; in the Northamptonshire *Zugodactylites* described herein, all the specimens, whether compressed or depressed, possess the characteristic sharp ventrolateral tubercles at the end of single ribs, at least at some stage of growth; in *Peronoceras* both compressed and depressed forms have fibulate ribs that are retained on the adult whorl; in the slightly stratigraphically younger *Porpoceras*, both compressed and depressed forms have the characteristic mixture of single and fibulate ribs with ventrolateral tubercles at intervals; and in Lincolnshire the population of *Dactylioceras commune* in the Commune Subzone contains a significant proportion of individuals with a remarkably large whorl breadth, which all, nevertheless, have the widely spaced, single, non-tuberculate primary ribs that are so characteristic of *D. commune*. The conclusion to be drawn is that the depressed-whorled forms are more closely related to the compressed-whorled forms that they accompany, than they are to the depressed-whorled forms in other zones. To maintain that the compressed and depressed-whorled types belong to two different lineages that are separate from the Tenuicostatum to the Variabilis Zones requires that a remarkable series of parallel evolutionary changes had to take place, with the same diagnostic characters evolving simultaneously in both lineages. This seems to be most unlikely, and it is much more probable that there is a close genetic relationship between the compressed and depressed forms at each horizon. In those cases where two different lineages do coexist at one horizon, such as the presence of *Peronoceras* and *Zugodactylites* in abundance in the Northamptonshire Fibulatum Subzone, then the differences between them are quite clear – each has its own diagnostic characters, there is no overlap in morphology, and there are no specimens that are intermediate between the two.

The classification adopted in each case depends on the quantity and state of preservation of the material. With the Grey Shales *Orthodactylites*, the abundant, well-preserved material allowed the continuity of the variation between very different end-forms to be demonstrated, so only one specific name was applied to each single-bed assemblage, and specific distinctions were used for significant changes from bed to bed. One of these changes involved severe restriction of the amount of variation in one species, *D. tenuicostatum*, which does not have the depressed forms of the preceding or succeeding species. Inevitably such a classification received severe criticism from Guex (1974), who would divide the assemblage at each horizon into *Dactylioceras* and *Nodicoeloceras*, thus arbitrarily splitting the continuous variation into two. In fact Guex's method is to decide in advance the scale and type of characters that are to be used for classification of Dactylioceratidae, then apply them to the Grey Shales collections, without taking account of proper analysis of the morphology of those collections. The different amount of variation in one of the Grey Shales species does not alter the basic reasons for treating each assemblage as a single species. Nor can the methods used be criticized because, according to Guex, *Nodicoeloceras* survived in the Bifrons Zone long after the disappearance of *Dactylioceras* – the depressed-whorled forms in the upper half of the Bifrons Zone are not *Nodicoeloceras*, they belong to *Porpoceras* or *Catacoeloceras*, or perhaps an unnamed genus. Another analysis that revealed a large amount of variation in a single species was Hirano's (1971 : 104–108) study of *Dactylioceras helianthoides* Yokoyama in Japan, where rib-density ranges at a given diameter were found to be as high as 3 : 1 between the most densely and most sparsely ribbed individuals from the same horizon. In the case of the *Peronoceras* and *Zugodactylites* faunas described here, the collections are not large enough to prove the continuity of the variation in each genus, and thus to refer all the forms at one horizon to a single species. Several species are used in each genus, this being the most practicable classification to adopt in this case. British collections of *Porpoceras* are treated in the same way.

After close examination of all the main occurrences of Dactylioceratidae in Britain, there seems no reason to change the basic classification of seven genera put forward previously (Howarth 1962*b* : 408), which is still the best expression of the sequence of changes that takes place in the Dactylioceratidae. The purely morphological approach of Buckman (1926–27 : 41–46) only confuses a relatively simple sequence of genera, as does the addition of a new generic name like *Rakusites* Guex (1971 : 232), which is based on a specimen of *Dactylioceras anguiforme* (Buckman), from the Falciferum Zone of Somerset, that has feebly tuberculate inner whorls. The total amount of variation in *D. anguiforme* is much more than the difference between the holotype (Buckman 1928 : pl. 763) and the specimen used as holotype of *Rakusites* (Guex 1971 : pl. 1, fig. 1). Such a morphological approach has led Guex (1973*b* : 575–581) to put forward a classification for Dactylioceratidae that is greatly at variance with the views expressed here. He separates all the depressed-whorled forms from the compressed-whorled forms that they accompany, then splits them up further so that there are long parallel lineages of *Catacoeloceras*, *Porpoceras* and *Nodicoeloceras*, all starting in the Tenuicostatum and Falciferum Zones. In my opinion *Catacoeloceras* starts in the Crassum Subzone, *Porpoceras* starts in the upper half of the Fibulatum Subzone and *Nodicoeloceras* starts in the Exaratum Subzone, and all Guex's records of these genera in older beds are based on misidentifications, as are also his records of *Collina* before the Fibulatum Subzone. The upper limits of these depressed-whorled genera are also clear in Britain and at Aveyron – the Commune Subzone for *Nodicoeloceras* and the top of the Fibulatum Subzone for *Porpoceras*, while *Catacoeloceras* ranges well up into the Variabilis Zone. However, it is not certain that all the depressed forms high in the Bifrons and Variabilis Zones in southern France and Italy can be satisfactorily accommodated in *Catacoeloceras* or *Collina*. *Transicoeloceras* Pinna (1966 : 124) has been applied to the most depressed forms in the Bifrons Zone in Italy, and *Platystrophites* Levi-Setti & Pinna (1971 : 476) is also available, though the latter may be a synonym of *Porpoceras*.

The Northamptonshire Dactylioceratidae do not provide any evidence for the recognition of dimorphism in the family, and the position remains as stated previously (Howarth 1973 : 249) – no collection from a British population contains adults that can be divided into two distinct groups which differ in size or any other morphological character. The evidence put forward by Guex (1973*b*) in support of dimorphism was obtained from collections of ammonites from the Bifrons Zone of the Aveyron area. All the specimens are pyritized phragmocones, mostly small and immature, in which the body chambers and mouth borders are not preserved. None of the specimens used (including those figured in the plates) show any adult features. The measurements given in a later paper (Guex 1974 : 423–425), as detailed evidence in support of dimorphism in one particular case, do not demonstrate that two groups were present. When the measurements are plotted as graphs, it can be seen that this collection of separate whorls shows continuous variation, and it has been split arbitrarily by Guex into two parts that do not represent natural groups. Again no adults are present. At other localities in many different parts of Europe all the genera present at Aveyron attain much larger sizes before they show adult features, which usually consist of a contracted or constricted mouth border to the adult body chamber. The proof of dimorphism in Dactylioceratidae cannot be obtained from collections of small, pyritized, septate inner whorls like those at Aveyron. The least that is required to demonstrate dimorphism satisfactorily is a substantial collection of complete adult specimens from one horizon, that are provably adult because they have constricted mouth borders and approximated suture-lines, and which can be shown to be divisible into two distinct groups on the basis of the diameter at the adult mouth border, or on other major differences such as the shape of the mouth border. There are many such collections of Hildoceratidae, but none of Dactylioceratidae are known so far.

Genus *DACTYLIOCERAS* Hyatt 1867

Type species. *Ammonites communis* J. Sowerby 1815, designated ICZN Opinion 576, 1959.

Synonyms. *Arcidactylites* Buckman 1926 (type species: *A. arcus*[1]); *Microdactylites* Buckman 1926 (type species : *Ammonites attenuatus* Simpson 1855); *Anguidactylites* Buckman 1926 (type species : *A. anguiformis*); *Leptodactylites* Buckman 1926 (type species: *L. leptum*); *Peridactylites* Buckman 1926 (type species: *P. consimilis*); *Toxodactylites* Buckman 1926 (type species: *T. toxophorus*); *Vermidactylites* Buckman 1926 (type species: *Ammonites vermis* Simpson 1855); *Xeinodactylites* Buckman 1926 (type species: *Dactylioceras helianthoides* Yokoyama 1904); *Athlodactylites* Buckman 1927 (type species: *Ammonites athleticus* Simpson 1855); *Curvidactylites* Buckman 1927 (type species: *C. curvicosta*); *Koinodactylites* Buckman 1927 (objective synonym); *Nomodactylites* Buckman 1927 (type species: *N. temperatus*); *Parvidactylites* Buckman 1927 (type species: *P. parvus*); *Simplidactylites* Buckman 1927 (type species: *S. simplicicosta*); *Rakusites* Guex 1971 (type species: *R. pruddeni*); *Eodactylites* Schmidt-Effing 1972 (type species: *Dactylioceras pseudocommune* Fucini 1935).

Diagnosis. Evolute planulates or serpenticones, in which the whorl section varies between compressed and highly depressed and typically has flat sides. Ribs single or bifurcating, either annular or passing over the venter with forwards inclination. Ventrolateral tubercles absent or small, but larger tubercles or spines and occasional fibulate ribs occur on the inner whorls of some species.

Remarks. The earliest species occur in the Mediterranean area, perhaps first in the upper part of the Spinatum Zone and definitely in the Tenuicostatum Zone; thereafter species are common or abundant up to the top of the Commune Subzone, where the genus evolves into *Peronoceras*. In north-west Europe examples do not occur in the Spinatum Zone, *Dactylioceras* s.s. occurs rarely low in the Tenuicostatum Zone (e.g. Howarth 1973 : 253), then the subgenus *Orthodactylites* becomes abundant higher in the Tenuicostatum Zone and survives to at least the middle of the Falciferum Subzone. *Dactylioceras* s.s. first occurs again in Britain in the Exaratum Subzone, and becomes abundant in the Falciferum and Commune Subzones. The restricted subgenus *Dactylioceras* consists of those species in which single, annular ribs are absent or only occasional, and they do not have the depressed whorls of some examples of *Orthodactylites*. The well-known type species *D. commune* has characteristically widely-spaced primary ribs on a flat whorl side, and ventrolateral tubercles are absent or only rudimentary. The morphology of *D. pseudocommune* Fucini, the type species of *Eodactylites*, is so similar to that of *D. commune* that *Eodactylites* has to be placed in synonymy with the subgenus *Dactylioceras*, even though the age difference between the two is considerable, i.e. basal Tenuicostatum Zone and Commune Subzone. In fact *D. pseudocommune* has only slightly more angular whorls, straighter ribs, a lower rib-density and slightly more prominent ventrolateral tubercles than *D. commune*. The sequence of species of *Dactylioceras* in Yorkshire has already been described (Howarth 1962*b* : 408–409), and a particularly rich and variable fauna is present at Barrington, Somerset. This variation is in the tuberculation and rib-density of the inner whorls, and includes fibulate ribs and ventrolateral tubercles and spines of varying sizes. Several forms are worthy of specific but not generic names.

In addition to the species described below, the following Dactylioceratidae also occur in Northamptonshire:

1. *Dactylioceras* cf. *anguiforme* (Buckman) in the Abnormal Fish Bed. The material obtained is insufficient and too poorly preserved for accurate identification. It represents a normal species

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[1] All type species are by original designation, unless stated otherwise.

of *Dactylioceras* s.s., and those characters that can be seen agree with *D. anguiforme* (Buckman 1928 : pl. 763) from the Exaratum Subzone of Barrington, Somerset. It is not the same as *D.* (? *Orthodactylites*) *vermis* (Simpson) which occurs at this horizon in Yorkshire (Buckman 1913 : pl. 68), at Grantham, Lincolnshire, and at Barrington, Somerset (Buckman 1927 : pl. 68A). *D. crassiusculosum* (Simpson) in the Exaratum Subzone of Yorkshire (Buckman 1912 : pl. 62) is also different.

2. *Dactylioceras* also occurs in the Lower Cephalopod Bed, but no specimens were obtained that are specifically determinable.

3. *Dactylioceras* spp. in the Upper Cephalopod Bed. *D. commune* (J. Sowerby) is abundant, and specimens agree exactly with the Yorkshire holotype (Dean, Donovan & Howarth 1961 : pl. 72, fig. 5) and topotypes (Buckman 1927 : pls 707, 708). An example of small inner whorls from King's Sutton, Northamptonshire, was figured by Buckman (1926 : pl. 657) as *Arcidactylites arcus*. It agrees exactly with the inner whorls of *D. commune* and must be considered a synonym. Specimens with considerably greater rib-density, especially at diameters of more than 30 mm, also occur in the Upper Cephalopod Bed, and they agree with *D. praepositum* (Buckman 1927 : pl. 701). The Northamptonshire specimens of *D. commune* and *D. praepositum* are mostly incomplete and not so well preserved as the abundant and well-known Yorkshire population of the two species. *Nodicoeloceras* sp. indet. occurs rarely in this bed, but those obtained were too small and too poorly preserved to identify accurately.

Subgenus ***ORTHODACTYLITES*** Buckman 1926

Type species. *O. directum* Buckman 1926.

Synonyms. *Kryptodactylites* Buckman 1926 (type species: *Ammonites semicelatus* Simpson 1843); *Tenuidactylites* Buckman 1926 (type species: *Ammonites tenuicostatus* Young & Bird 1822); ? *Kedonoceras* Dagis 1968 (type species: *K. asperum*).

Diagnosis. *Dactylioceras* with annular, rectiradiate or prorsiradiate ribs. Single as well as bifurcating ribs occur commonly at some growth stage. Rib-density moderate to high, occasionally distantly ribbed on inner whorls. Whorl shape varies from compressed to highly depressed. Ventrolateral tubercles or spines may occur on depressed whorls and ribs may be looped to them in fibulate style.

Remarks. Species of *Dactylioceras* with a mixture of single and bifurcating annular ribs on at least their outer whorls occur throughout much of the Tenuicostatum Zone, and the rich faunas in the Grey Shales of Yorkshire have been described previously (Howarth 1973). Although they are largely superseded by *Dactylioceras* s.s. in the Falciferum Zone, some species of *Orthodactylites* remain, and one of them, the new species *D.* (*O.*) *semiannulatum*, occurs in the Exaratum and Falciferum Subzones of Northamptonshire. It has a wide distribution from Yorkshire to Somerset, and those specimens in the Falciferum Subzone are probably the youngest *Orthodactylites* in England.

Dactylioceras* (*Orthodactylites*) *semiannulatum sp. nov.

Pl. 1, figs 1–9

1927 *Xeinodactylites helianthoides* (Yokoyama); Buckman : pl. 699.
1927 *Dactylioceras annulatum* (J. Sowerby); Buckman : pl. 700.
1962*b* *Dactylioceras* sp. nov. Howarth : 387, bed 37.
? 1973*a* *Dactylioceras aequistriatum* (Zieten); Guex : 508; pl. 11, fig. 7; pl. 14, fig. 13.

Diagnosis. A species with rounded whorls, annular ribs and no tubercles that occurs in the Falciferum Zone. The whorl section is nearly circular and the whorl breadth slightly exceeds the height. The ribs are straight, annular and radial or slightly rursiradiate; many bifurcate at the ventrolateral position, but at diameters of more than 40 mm single ribs are also common.

Holotype. BM C.71280 from the Abnormal Fish Bed, Exaratum Subzone, 1·5 km north of Byfield, Northamptonshire.

OTHER MATERIAL. Paratypes from the same bed and locality as the holotype are C.70856–59 and C.71281–83. Other paratypes from Somerset, Leicestershire and Yorkshire are listed below.

DIMENSIONS. These are given in the following order. Diameter: whorl height, whorl breadth, umbilical width; the figures in brackets express the last three dimensions as proportions of the diameter.

C.71280 – 52·0: 15·3 (0·29), 16·4 (0.32), 24·0 (0·46)
C.70856 – 59·0: 16·6 (0·28), 17·5 (0·30), 28·7 (0·49)
C.70858 – 37·4: 12·0 (0·32), 13·0 (0·35), 16·3 (0·44)
C.71924 – 30·0: 10·3 (0·34), 14·0 (0·47), 12·5 (0·42)

DESCRIPTION. The known material of this species comes from the Abnormal Fish Bed at Byfield, Northamptonshire; a bed of nodules 12 m above the Marlstone Rock Bed, 1·3 km south of Harston, Leicestershire (SK 840305); bed 37 at Port Mulgrave, Yorkshire coast (Howarth 1962*b* : 387); and bed 6 at Barrington, Somerset (Pringle & Templeman 1922 : 451); all are of Exaratum Subzone age. It also occurs in bed 18/19 at the latter locality, of lower Falciferum Subzone age. The specimens from Byfield include one that is 75 mm in diameter at the broken aperture of its body chamber which is one whorl in length, and it may have been a complete adult. The other specimens are smaller, but better preserved, and they show the inner whorls down to about 10 mm diameter (Pl. 1, figs 1–3, 9). The Harston specimen (Pl. 1, fig. 6) is a small individual of 30 mm diameter with fairly thick whorls. The Port Mulgrave specimens are those recorded previously (Howarth 1962*b*) as *Dactylioceras* sp. nov. (C.50206, C.50210–18). They are also small specimens of up to 50 mm diameter, and include the three inner whorls figured here (Pl. 1, figs 4, 5, 7), which show variation in whorl thickness at 28 mm diameter from 0·37 to 0·43 of the diameter. The holotype has 62 ribs on its last whorl at 56 mm diameter. Some specimens (e.g. Pl. 1, fig. 1) have slightly more ribs, and the Port Mulgrave specimens' inner whorls are fairly fine-ribbed, but there is no large variation in the rib-density of this species, as in some others (Howarth 1973). The specimen from bed 6 at Barrington figured by Buckman (1927 : pl. 699) is similar in most respects, though it has slightly fewer ribs on its innermost whorls. The Falciferum Subzone example from bed 18/19 at Barrington (Buckman 1927 : pl. 700) is 78 mm in diameter, with a body chamber of just less than one whorl in length, and compares closely with the Byfield specimens in whorl dimensions and rib-density. Another specimen (Pl. 1, fig. 8) from the same district, from Moolham, Ilminster, and probably from the Falciferum Subzone, is similar. It has a body chamber exactly one whorl in length ending in a constricted and flared mouth border at about 93 mm diameter, showing it to be an adult. The species is referred to the subgenus *Orthodactylites* because of the substantial number of single ribs, especially at diameters of more than 40 mm; it is the youngest known species of that subgenus.

Nodicoeloceras crassoides occurs in the same beds at all the localities, and can be distinguished from *D. semiannulatum* by its much larger whorl breadth and by the tubercles that are usually present on its inner whorls. The greatest resemblance, however, is with *D. semicelatum* (Simpson) in the top subzone of the Tenuicostatum Zone. *D. semicelatum* has a very large variation in whorl breadth, rib-density and presence or absence of tubercles, and the ribs are prorsiradiate or occasionally radial. In *D. semiannulatum* the ribs vary between radial and rursiradiate, and specimens are not continuously variable into the depressed-whorled contemporaneous species *Nodicoeloceras crassoides*. *D. helianthoides* Yokoyama, with which Buckman identified one of the Barrington ammonites, has been redescribed by Hirano (1971 : 104; pl. 14, figs 1–10); it belongs to the

Plate 1 ×1

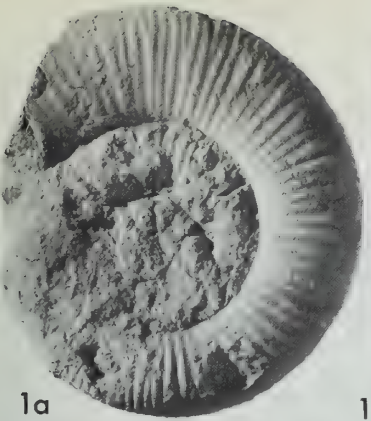
Dactylioceras (*Orthodactylites*) *semiannulatum* sp. nov., Exaratum Subzone

Figs 1–3, 9. Abnormal Fish Bed, quarry at Iron Cross Farm, 1·5 km north of Byfield, Northamptonshire. Fig. 1, BM C.70856. Fig. 2, holotype, BM C.71820. Fig. 3, BM C.70858. Fig. 9, BM C.70857.

Figs 4, 5, 7. Bed 37, Jet Rock, Rosedale Wyke, Port Mulgrave, Yorkshire. Fig. 4, BM C.50214. Fig. 5, BM C.50218. Fig. 7, BM C.50212.

Fig. 6. Nodules 12 m (40 ft) above Marlstone Rock Bed, quarry (SK 840305), 1·2 km south of Harston, Leicestershire; BM C.71924.

Fig. 8. Moolham Farm, Ilminster, Somerset; BM C.72558.



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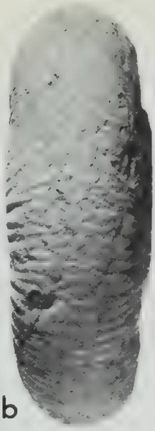

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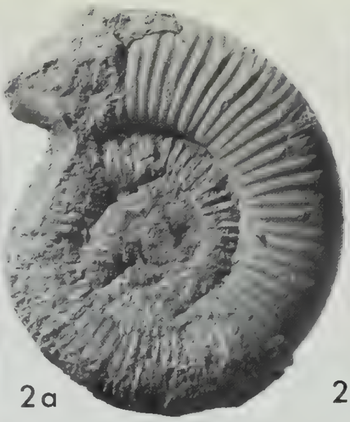

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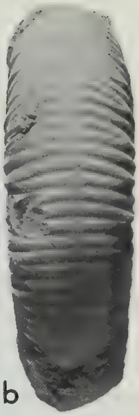

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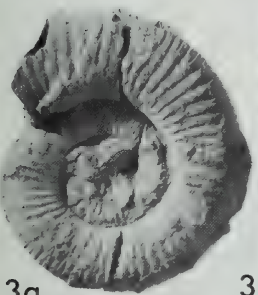

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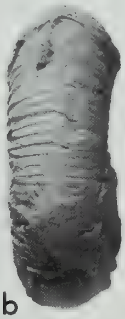

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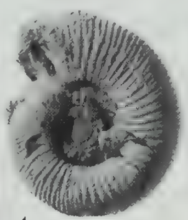

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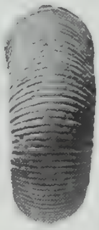

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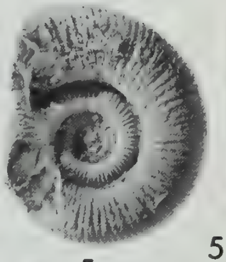

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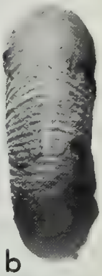

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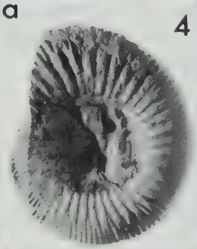

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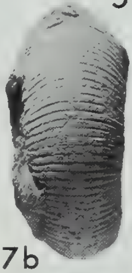

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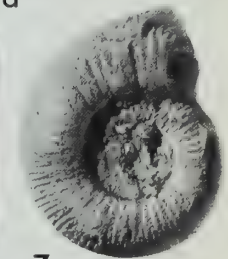

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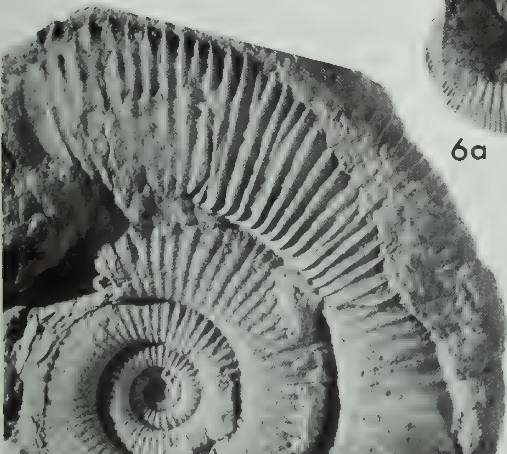

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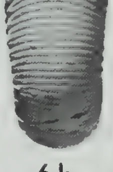

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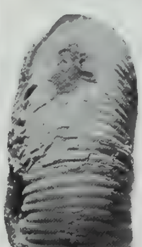

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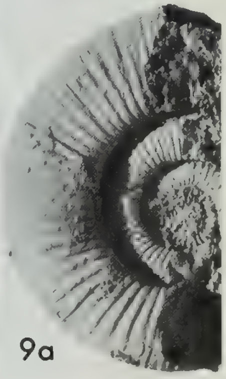

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subgenus *Dactylioceras* s.s., has few or no single ribs, and has ventrolateral tubercles on the inner whorls. The specimen from Morocco figured by Guex (1973*a* : 508; pl. 11, fig. 7) as *D. aequistriatum* (Zieten) appears to be very close to *D. semiannulatum*. Its identification cannot be upheld until a suitable type specimen is obtained for Zieten's species.

Genus *NODICOELOCERAS* Buckman 1926

Type species. *Ammonites crassoides* Simpson 1855.

Synonymy. *Crassicoeloceras* Buckman 1926 (type species: *C. pingue*); *Lobodactylites* Buckman 1926 (type species: *L. lobatum*); *Multicoeloceras* Buckman 1926 (type species: *M. multum*); *Spinicoeloceras* Buckman 1926 (type species: *S. spicatum*); *Mesodactylites* Pinna & Levi-Setti 1971 (type species: *M. annulatiforme*).

Diagnosis. Whorls always depressed, with wide flat or arched venter, and inner whorls often cadicone. Ribs usually bifurcate at ventrolateral edge, occasionally single, and sometimes fibulate in tuberculate specimens. Rib-density moderate to low. Development of ventrolateral tubercles or spines on inner whorls very variable, tubercles absent in some species.

Remarks. The type species occurs in the upper half of the Exaratum Subzone, and others occur in the Falciferum and Commune Subzones, especially in the Barrington area of Somerset. The development of tubercles is particularly variable in this genus: in some cases they occur as intermittent spines with non-tuberculate ribs between, or they may be developed on every rib, or ribs may be looped in pairs to them (fibulate), while in other species tubercles are present in some individuals but absent in others. The combination of variable tuberculation and highly depressed whorls makes the genus distinctive and worthy of separation from *Dactylioceras*. Some complete adults are known in which the final whorl contracts in breadth up to the mouth border (e.g. Pl. 3, fig. 1), but they do not become compressed as in *Dactylioceras*. The depressed whorls are, therefore, a feature of all growth stages of *Nodicoeloceras*.

Nodicoeloceras crassoides (Simpson 1855)

Pl. 2, figs. 1, 4, 5; Pl. 3, fig. 1

1819 *Ammonites annulatus* J. Sowerby : 41; pl. 222, fig. 5 (*non* figs 1–4) (*non Ammonites annulatus* Schlotheim 1813).
1855 *Ammonites crassoides* Simpson : 55.
1855 *Ammonites fonticulus* Simpson : 57.
1884 *Stephanoceras subarmatum* (Young & Bird); Wright : 477; pl. 85, figs 2, 3.
1884 *Stephanoceras raquineanum* (d'Orbigny); Wright : 478; ? pl. 86, figs 5–7; pl. 87, figs 7, 8.
1885 *Stephanoceras raquineanum* (d'Orbigny); Thompson : 307; pl. 1, figs 2, 2a.
1912 *Coeloceras fonticulum* (Simpson) Buckman : pl. 59.
1913 *Coeloceras crassoides* (Simpson) Buckman : pl. 89.
1927 *Nodicoeloceras crassoides* (Simpson) Buckman : pl. 89A.

Plate 2 ×1

Nodicoeloceras crassoides (Simpson), Exaratum Subzone

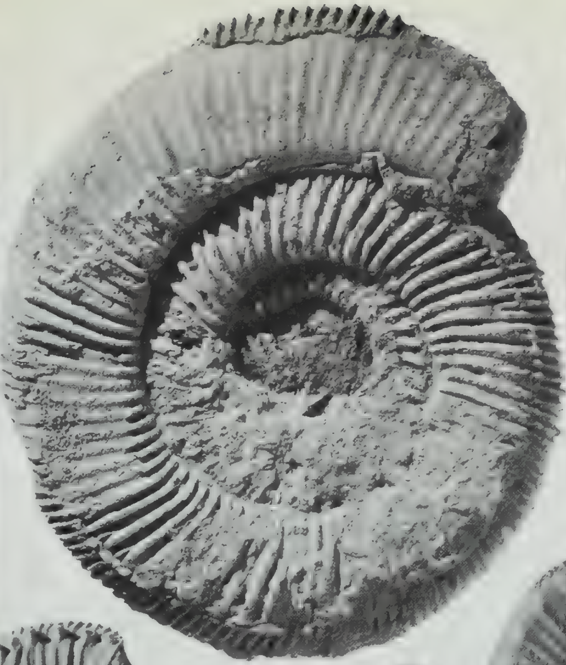
Figs 1, 4, 5. Abnormal Fish Bed. Fig. 1, Catesby, 6·5 km south-west of Daventry, Northamptonshire; Northampton Museum, B. Thompson collection. Fig. 4, quarry at Iron Cross Farm, 1·5 km north of Byfield, Northamptonshire; BM C.70862. Fig. 5, Byfield, Northamptonshire; BM C.69088, W. E. Cutler Colln.

Peronoceras fibulatum (J. de C. Sowerby), Fibulatum Subzone

Fig. 2. Lower *Leda ovum* Beds, Thenford Hill, 7 km north-east of Banbury, Northamptonshire; OUM J.20184, T. Beesley Colln.

Peronoceras turriculatum (Simpson), Fibulatum Subzone

Fig. 3. Bed 63, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.68125.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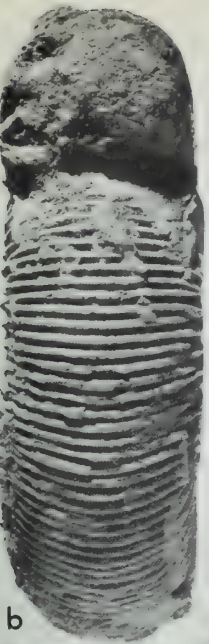
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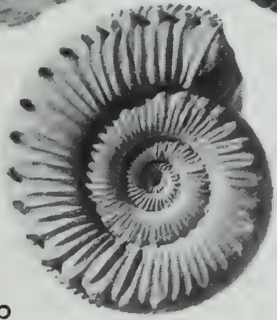
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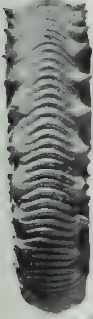
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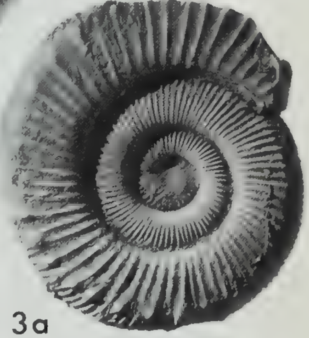
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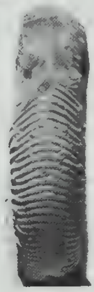
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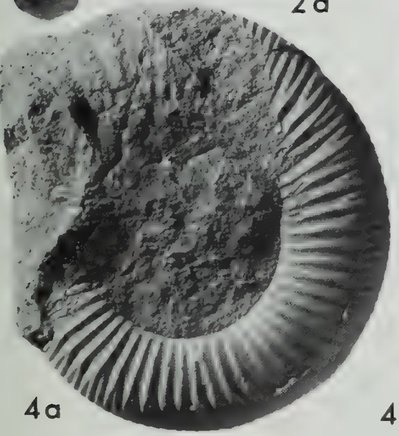
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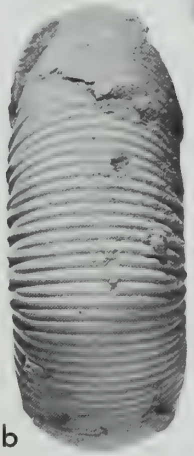
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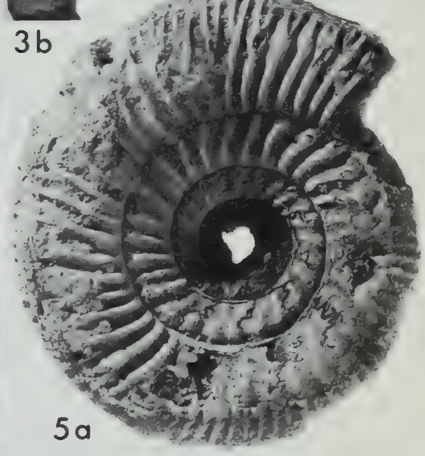
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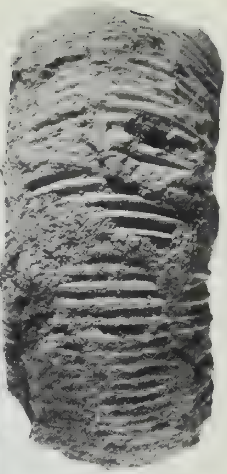
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1927 *Crassicoeloceras pingue* Buckman : pl. 728.
1963 *Nodicoeloceras crassoides* (Simpson); Zanzucchi : 117; pl. 14, figs 8, 8a.
1963 *Catacoeloceras crassoides* (Simpson) Sapunov : 126; pl. 5, fig. 2; pl. 6, fig. 1.
1963 *Catacoeloceras fonticulum* (Simpson) Sapunov : 126; pl. 6, fig. 2.
1968 *Nodicoeloceras crassoides* (Simpson); Lehmann : 53; pl. 17, fig. 4.
1971 *Nodicoeloceras crassoides* (Simpson); Pinna & Levi-Setti : 99; pl. 4, figs 1, 2.
1972 *Nodicoeloceras crassoides* (Simpson); Schmidt-Effing : 122; pl. 13, fig. 4; pl. 14, fig. 2.
? 1973 *Nodicoeloceras crassoides* (Simpson); Weitschat : 38; pl. 1, fig. 4.

HOLOTYPE. Whitby Museum no. 126 (Buckman 1913 : pl. 89), from the Exaratum Subzone of the Yorkshire coast.

DIMENSIONS.

Holotype	– 76·0: 19·0 (0·25), 27·4 (0·36), 39·5 (0·52)
Pl. 2, fig. 1	– 92·5: 23·7 (0·25), 26·6 (0·29), 46·1 (0·50) – 60·5: 19·1 (0·32), 26·3 (0·43), 27·8 (0·46)
C.69088	– 64·5: 18·6 (0·29), 27·2 (0·42), 31·4 (0·49)
BM 43894	– 103·0: 24·5 (0·24), 30·0 (0·29), 56·0 (0·54) – 70·0: 21·6 (0·31), 32·8 (0·47), 32·2 (0·46)

DESCRIPTION. *Nodicoeloceras crassoides* occurs commonly in the Abnormal Fish Bed and in the Inconstant Cephalopod Bed, associated with *Dactylioceras* (*Orthodactylites*) *semiannulatum* described above. There is some resemblance between the two species, but *N. crassoides* always has a much larger whorl breadth, and ventrolateral tubercles are usually developed on its inner whorls. No specimens transitional between the two species have been found. The Northamptonshire population of *N. crassoides* shows considerable variation in whorl dimensions, rib-density and size of tubercles, and the presence or absence of the shell accounts for the entirely different appearance of the sharp, high ribs and tubercles of the shell and the low almost effaced ribs on the internal mould (Pl. 2, fig. 1) (Howarth 1975). A specimen with its shell complete, from the Abnormal Fish Bed of Chipping Warden, Northamptonshire, was figured by Wright (1884 : pl. 85, figs 2, 3); it has widely-spaced ribs, ventrolateral tubercles on its inner whorls, a particularly large whorl breadth and some fibulation on the inner whorls. A similar Byfield specimen is figured in Pl. 2, fig. 5, although this has no fibulate ribs. Every gradation exists between this coarse-ribbed, wide-whorled type and the median form figured in Pl. 2, fig. 1. Specimens obtained from the unweathered Abnormal Fish Bed at Iron Cross quarry, Byfield, rarely have any shell attached; such a specimen, with relatively slender whorls and no tubercles at the smallest diameter seen, is figured in Pl. 2, fig. 4, to illustrate the opposite end of the morphological range. Specimens also occur in the Lower Cephalopod Bed, such as the example from Watford, west Northamptonshire, figured by Thompson (1885 : 309; pl. 1, figs 2, 2a), showing that the species occurs in both subzones of the Falciferum Zone in Northamptonshire. On the Yorkshire coast *N. crassoides* occurs in bed 37 (Howarth 1962*b* : 387) in the upper part of the Exaratum Subzone, associated with *D. vermis* (Simpson), *D. crassiusculosum* (Simpson) and *D. semiannulatum* sp. nov. The holotypes of *N. crassoides* itself and of its synonym *Ammonites fonticulus* Simpson came from this bed; both specimens have a large whorl breadth and tubercles on their inner whorls, and others collected from the same bed show a morphological range similar to that of the Northamptonshire specimens.

At Barrington, Somerset, *N. crassoides* occurs in bed 7, at about the middle of the Exaratum Subzone, and also in beds 16 and 18/19 (Pringle & Templeman 1922 : 451) in the Falciferum Subzone. The best specimens are from bed 18/19: two of them were figured by Buckman (1927 : pls 89A, 728), and one (pl. 728) was made the holotype of the new genus and species *Crassicoeloceras pingue*. They both are very closely comparable with the Yorkshire and Northamptonshire specimens and are in fact conspecific. Another specimen that is conspecific is the lectotype of *Ammonites annulatus* (J. Sowerby 1819 : 41; pl. 222, fig. 5), also from the Ilminster–Barrington succession. Oppel (1856 : 255), Tate & Blake (1876 : 299) and Wright (1884 : 473) all restricted Sowerby's species to his fig. 5 of pl. 222, and excluded his figs 1–4, but none of these was a formal selection of the lectotype, which must be attributed to Sylvester-Bradley (1958 : 67). The other three figured paralectotypes of Sowerby's *A. annulatus* are an example of *Dactylioceras semicelatum* (Simpson) from the top of the Marlstone Rock Bed at Copredy, Northamptonshire (Sowerby 1819 : pl. 222, fig. 1), another of the same species from the Grey Shales of the Yorkshire coast (pl. 222, fig. 2), and a *D. anguiforme* (Buckman) from the Falciferum Zone, ? Exaratum Subzone, of Ilminster, Somerset (pl. 222, figs 3, 4). As was mentioned in an earlier paper (Howarth 1973 : 257), the lectotype agrees exactly in matrix with other ammonites from bed 18/19 at Barrington, and it is a large specimen with a complete adult body chamber 1¼ whorls long (Pl. 3, fig. 1). On its outer whorl there is a mixture of single and bifurcating ribs, while on the penultimate whorl down to a diameter of about 45 mm all the ribs bifurcate and ventrolateral tubercles are present on most of them. It has a high whorl breadth throughout.

A. annulatus J. Sowerby 1819 cannot be used as the specific name instead of *N. crassoides* Simpson 1855, because it is preoccupied by *Ammonites annulatus* Schlotheim 1813. Tate & Blake (1876 : 168) and Wright (1884 : pl. 84, figs 7, 8) both interpreted Sowerby's species as an important index-species for the lowest zone of the Upper Lias, a mistake that was corrected by Buckman (1910*a* : 85), who pointed out that the correct determination for that completely different compressed-whorled index-species was *Dactylioceras tenuicostatum*. Another *Nodicoeloceras* that occurs in the Falciferum Zone is *N. spicatum* (Buckman 1928 : pl. 777) in bed 23 at Barrington, and *N. lobatum* (Buckman 1927 : pl. 730) and *N. multum* (Buckman 1928 : pl. 785) occur in the overlying Commune Subzone; they all differ in details of ribbing or tuberculation.

Genus *PERONOCERAS* Hyatt 1867

TYPE SPECIES. *Ammonites fibulatus* J. de C. Sowerby 1823, subsequently designated by Buckman (1911 : *v*).

DIAGNOSIS. Gradational from compressed ellipsocones to depressed cadicones. Whorls quadrangular with flat sides and venter. Ribs fine to distant; regular fibulation to ventrolateral tubercles or spines always present at some growth stage, but may be absent on small whorls of fine-ribbed species.

DISTRIBUTION. Fibulatum Subzone, lower and middle parts. Northamptonshire: Unfossiliferous Beds (top 4·6 m), Lower and Middle *Leda ovum* Beds. Yorkshire: Whitby beds 60–63, Ravenscar beds xxix and xxx.

REMARKS. *Peronoceras* is best known from its development on the Yorkshire coast. At Whitby it occurs in large numbers in a restricted group of beds (Howarth 1962*b* : 397, beds 60–63) that directly overlie the Commune Subzone containing *Dactylioceras athleticum* (Simpson) and *D. praepositum* (Buckman). In Northamptonshire it has similar relationships with the highest species of *Dactylioceras*, and again there is no overlap between the two genera. Fibulation combined with compressed whorls is the diagnostic feature of *Peronoceras*, but fibulation is by no means confined to *Peronoceras*, for many depressed-whorled Dactylioceratidae in other parts of the Upper Lias have ribs looped to tubercles or spines on their inner whorls. *Porpoceras* also has fibulate ribs in species that have depressed or approximately square whorls, but in that genus the mixture of fibulate and single ribs is distinctive, and in Britain it occurs at a higher horizon.

Large collections from single horizons in the Yorkshire Fibulatum Subzone show many intermediates between entirely different end-forms. The series between compressed fine-ribbed and depressed coarse-ribbed runs from *P. turriculatum* to *P. fibulatum* and then *P. subarmatum*. Unlike the Tenuicostatum Zone fauna of *Dactylioceras* (*Orthodactylites*) described earlier (Howarth 1973), these species of *Peronoceras* retain differences up to the end of the adult body chamber. Complete specimens of the three species differ from each other at all growth stages, so there is justification for maintaining that three species coexisted at the same horizon. Placing them all under one specific name would unite specimens that are always different; 'splitting' or 'lumping' has no stratigraphical significance for the full range of morphologies occurs throughout the stratigraphical range of the genus in Yorkshire and probably in Northamptonshire. *P. perarmatum* (including *P. andraei*) differs in having widely-spaced ribs at all growth stages and a whorl section that varies from square to depressed. There is, however, no justification for dividing off those species with depressed whorls as a different genus, because the complete range from compressed to depressed occurs together, they evolve and die out at the same horizons, and they have characters of consistent fibulation in common that unite them and mark them off from other older and younger genera. The link with the ancestral species *D. praepositum* (Buckman) in the beds directly below is through the fine-ribbed compressed species *Peronoceras turriculatum*, which differs only slightly in possessing fibulate ribs.

As in other Dactylioceratidae, adult *Peronoceras* have a constriction at the mouth border. Occasional examples have an earlier constriction in the last half whorl of the adult body chamber (e.g. Pl. 3, fig. 2; Pl. 5, fig. 3), and these are probably individuals that grew again after the first onset of sexual maturity. The mean diameter at the adult mouth border in 15 specimens of *P. fibulatum* is 81 mm, the range being 65–100 mm. The other species become adult within the same range, though the mean adult diameter may be slightly larger in *P. turriculatum*, and slightly smaller in *P. subarmatum* and *P. perarmatum*. All complete adults have body chambers between $\frac{13}{16}$ and 1 whorl in length. Only one much smaller specimen has been found so far: an example of *P. subarmatum* (Pl. 4, fig. 4) which is complete and apparently adult at 23 mm diameter. It has some injuries and irregular ornament on the outer whorl, and it is not proposed to claim that dimorphism can be recognized in *Peronoceras* on the evidence of this specimen alone.

Peronoceras fibulatum (J. de C. Sowerby 1823)

Pl. 2, fig. 2; Pl. 3, fig. 2; Pl. 4, figs 1, 2

1823 *Ammonites fibulatus* J. de C. Sowerby : 147; pl. 407, fig. 2.
1830 *Ammonites bollensis* Zieten : 16; pl. 12, fig. 3.
1885 *Ammonites bollensis* Zieten; Quenstedt : 370; pl. 46, fig. 14.
1926 *Peronoceras fibulatum* (J. de C. Sowerby) Buckman : pl. 683.
1961 *Peronoceras fibulatum* (J. de C. Sowerby); Dean, Donovan & Howarth : pl. 73, fig. 2.
1963 *Peronoceras fibulatum* (J. de C. Sowerby); Sapunov : 128; pl. 6, fig. 3.
1966 *Peronoceras fibulatum* (J. de C. Sowerby); Fischer : 36; pl. 1, fig. 15; pl. 5, fig. 11.
? 1968 *Peronoceras fibulatum* (J. de C. Sowerby); Lehmann : 54; pl. 17, fig. 2.

Lectotype. BM 43911 from Whitby, Yorkshire (figured Sowerby 1823 : pl. 407, fig. 2; Dean, Donovan & Howarth 1961 : pl. 73, fig. 2), is one of three syntypes in Sowerby's collection. Although is it the specimen Sowerby figured, it is a syntype and not the holotype. It is here designated lectotype. The other two syntypes, now paralectotypes, are also both *P. fibulatum* from Whitby: C.79626 is 80 mm in diameter and is a complete adult, but most of the venter is worn away on the whole of the outer whorl, so it would not be suitable as a lectotype; C.79627 is only 27 mm in diameter.

Diagnosis. Whorl section compressed to approximately square. Ribs of moderate density and looped in pairs to ventrolateral tubercles, though occasional single ribs may occur on outer whorls. Two ribs issue from each ventrolateral tubercle and are projected forwards on the venter.

Description. *P. fibulatum* is the commonest species of *Peronoceras* in Britain, and is characterized by evolute, square to compressed whorls, moderate rib-density, and a high proportion of ribs looped in pairs (fibulation) to ventrolateral tubercles. Other species of *Peronoceras* have different whorl proportions and rib-densities, and less consistent fibulation. The Yorkshire coast lectotype is an evolute, almost serpenticone, and densely-ribbed specimen, and is fibulate throughout. The other end of the variation in the species is illustrated by another Yorkshire specimen, figured in Pl. 4, fig. 1, which has more massive whorls and more widely spaced ribs. Many other Yorkshire

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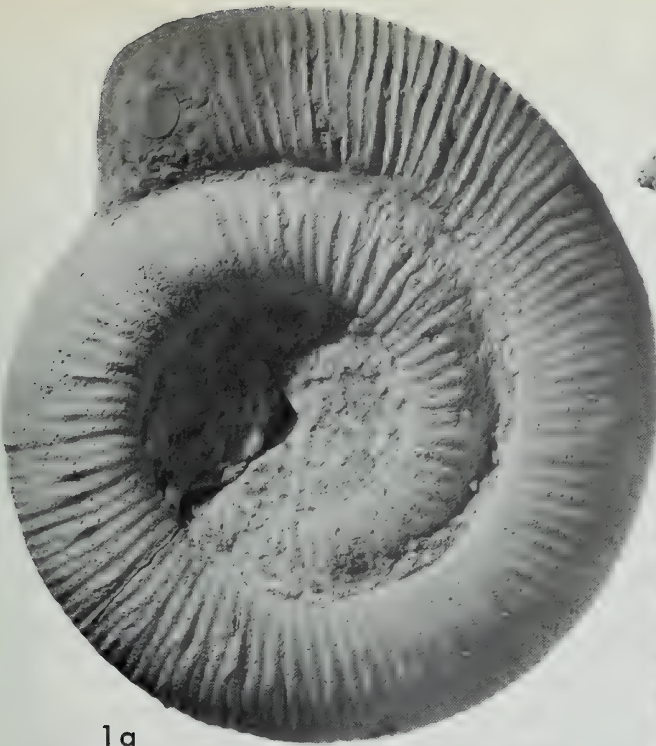
Plate 3 ×1

Nodicoeloceras crassoides (Simpson), [Falciferum Subzone]
Fig. 1. [Bed 18/19, Barrington], Ilminster, Somerset; BM 43894 (lectotype of *Ammonites annulatum* J. Sowerby, 1819 : 41; pl. 222, fig. 5).

Peronoceras fibulatum (J. de C. Sowerby), Fibulatum Subzone
Fig. 2. *Leda ovum* Beds, Northampton; BM C.67519.

Peronoceras turriculatum (Simpson), Fibulatum Subzone
Fig. 3. Bed 63, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.56567.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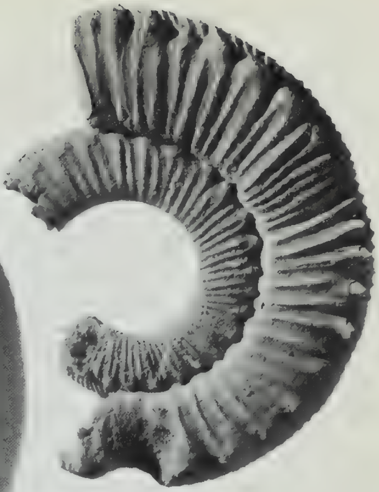
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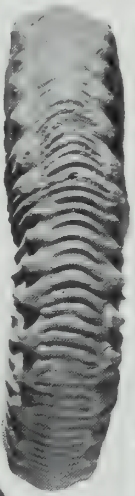
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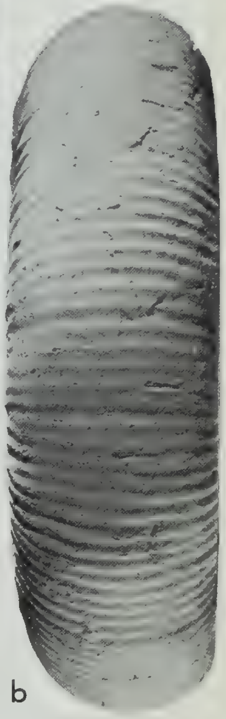
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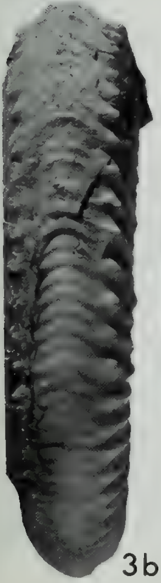
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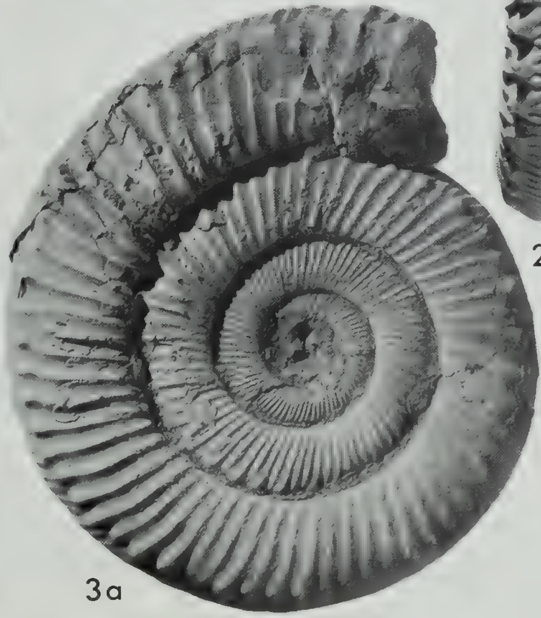
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specimens fall within this range of variation, including the example figured by Buckman (1926 : pl. 683).

In Northamptonshire *P. fibulatum* occurs in the top 4·6 m of the Unfossiliferous Beds and in the Lower and Middle *Leda ovum* Beds. Specimens were fairly common at some localities, especially former brickpits in Northampton. The range of morphology they exhibit is similar to those from the Yorkshire coast: Pl. 3, fig. 2 shows a specimen of average whorl dimensions and rib-density, and Pl. 4, fig. 2 an example with more widely-spaced ribs. Most specimens are preserved as internal moulds or with only the inner shell intact (Howarth 1975), and the relief of the ribs and especially the ventrolateral tubercles is much reduced. On the adoral half of body chambers, however, the inner shell is not developed, and the tubercles are seen to be sharply pointed spines when the main shell is preserved (Pl. 2, fig. 2).

Ammonites bollensis Zieten (1830 : 16; pl. 12, fig. 3), including the specimen figured under that name by Quenstedt (1885 : pl. 46, fig. 14), is a synonym of *P. fibulatum*. *Ammonites youngi* Reynès (1879 : pl. 3, figs 13–18) is probably also a synonym, but it will be necessary to select and figure a type specimen before that specific name can be definitely interpreted.

Peronoceras turriculatum (Simpson 1855)

Pl. 2, fig. 3; Pl. 3, fig. 3; Pl. 4, figs 3, 6, 8

1855 *Ammonites turriculatus* Simpson : 59.
1911 *Peronoceras turriculatum* (Simpson) Buckman : pl. 30.
? 1968 *Dactylioceras attenuatum* (Simpson); Lehmann : 49; pl. 17, fig. 8.
? 1972 *Dactylioceras* sp. indet. 2, Guex : 618; pl. 8, figs 5, 8, 9.
? 1972 *Microdactylites attenuatus* (Simpson); Guex : 618; pl. 8, fig. 7.

HOLOTYPE. Whitby Museum no. 152, figured by Buckman (1911 : pl. 30).

DIAGNOSIS. Whorls compressed with flat sides and arched venter. Ribs fine and dense up to 40 mm diameter, and occasionally looped in pairs to ventrolateral tubercles; at larger diameters ribs are stronger and fibulation becomes more prominent, but some single ribs without tubercles remain. Most ribs bifurcate at the ventrolateral shoulder, and are projected forwards on the venter and sometimes raised in the middle.

DESCRIPTION. *P. turriculatum* differs from *P. fibulatum* in having fine dense ribs on the inner whorls, and only a few fibulate ribs. The dense ribs occur up to about 40 mm diameter, and there are occasional small ventrolateral tubercles to which the ribs are looped. The ribs bifurcate at the ventrolateral shoulder and form secondary ribs that are projected forwards over the arched venter. At larger sizes the ribs become more widely spaced, and fibulation is more frequent. On the body chamber ventrolateral tubercles are sometimes developed on each rib, and specimens have the appearance of a large, thick-whorled and coarsely-ribbed *Zugodactylites braunianus*. *P. turriculatum* shows considerable variation in development of tubercles and fibulation, but rib-density is greater throughout than in most examples of *P. fibulatum*.

In Yorkshire *P. turriculatum* is fairly common throughout the *Peronoceras*-bearing part of the Fibulatum Subzone, and the holotype is a median member of the species in all characters. A more complete adult Yorkshire specimen that shows the single ribs with ventrolateral tubercles on the body chamber is figured in Pl. 3, fig. 3, and an example of the densely-ribbed inner whorls is figured in Pl. 2, fig. 3. Specimens are somewhat smaller and usually less complete in Northamptonshire, where they occur in the top part of the Unfossiliferous Beds and in the Lower *Leda ovum* Beds. Two examples of densely ribbed inner whorls are figured in Pl. 4, figs 3 and 6, one almost without tubercles, the other with small sharp tubercles, and a larger specimen with more widely-spaced ribs and much larger tubercles on the outer whorl is figured in Pl. 4, fig. 8.

Peronoceras subarmatum (Young & Bird 1822)

Pl. 4, figs 4, 5, 7

1822 *Ammonites subarmatus* Young & Bird : 250; pl. 13, fig. 3.
1855 *Ammonites semiarmatus* Simpson : 60.

1962*a* *Peronoceras subarmatum* (Young & Bird) Howarth : 117; pl. 17, fig. 5.
1962*a* *Peronoceras semiarmatum* (Simpson) Howarth : 117; pl. 17, fig. 6.
1966 *Peronoceras subarmatum* (Young & Bird); Fischer : 37; pl. 1, figs 16, 17; pl. 5, fig. 12; pl. 6, figs 1–3.

NEOTYPE. Whitby Museum no. 521 was described, figured and designated neotype by Howarth (1962*a* : 117; pl. 17, fig. 5), though it is possible that this specimen is the holotype.

DIAGNOSIS. Whorls depressed, with whorl height/whorl breadth ratio of 0·65–0·85 at 35–50 mm diameter. On the coronate inner whorls almost all ribs are looped in pairs to large ventrolateral tubercles or spines. A few single ribs without tubercles occur on the outer whorl. Two ribs issue from each tubercle and cross the venter with only slight forwards projection.

DESCRIPTION. Specimens with slightly to much depressed whorl sections, and coronate inner whorls where the ribs are looped to long ventrolateral spines, also often accompany *P. fibulatum*. The depressed whorl section remains in the adult body chamber, and so these forms are referred to a separate species, *P. subarmatum*. The neotype from Whitby has approximately average depressed whorls in which the ratio of whorl height to whorl breadth is 0·85 at 50 mm diameter. Another Whitby specimen, the neotype of *Ammonites semiarmatus* Simpson (Howarth 1962*a* : 117; pl. 17, fig. 6), has slightly less depressed whorls, but is similar in all other characters, and is therefore placed in synonymy with *P. subarmatum*. *P. perarmatum* has more widely-spaced ribs throughout growth.

Most of the Northamptonshire specimens are less complete, and consist mainly of inner whorls or immature examples with body chambers. Two such immature specimens are figured (Pl. 4, figs 5, 7), both with one whorl of body chamber, but the mouth borders are missing. In both, the fibulate tuberculate ribs of the inner whorls give way to a mixture of fibulate, single tuberculate and single non-tuberculate ribs on the last $\frac{1}{4}$ whorl. These are modifications usually associated with an adult body chamber, so the complete adult diameter of these specimens would probably have been about 60–70 mm. A much smaller complete adult specimen is also known from Bugbrooke, Northamptonshire, which is one of the main localities from which *P. subarmatum* has been obtained (Pl. 4, fig. 4). It is only 23 mm in diameter at the constricted mouth border, the body chamber is $\frac{3}{4}$ whorl in length and the final two closely approximated septa occur at 16 mm diameter. Whorl dimensions (mm) just before the mouth border are 22·0: 6·4 (0·29), 8·1 (0·37), 11·0 (0·50) (whorl height/breadth ratio 0·74); at smaller sizes the whorls are more depressed, e.g. at 14 mm diameter whorl height/breadth ratio is 0·51. On the small parts of the penultimate whorl that are exposed, large ventrolateral tubercles with some single and some fibulate ribs can be seen. On the final $\frac{3}{4}$ whorl the ribs and tubercles become irregular, most of the tubercles on one side of the whorl do not correspond with those on the other side, and there are signs of injury on the early part of the body chamber. It is possible that this specimen stopped growing or became prematurely adult because of its injuries.

Peronoceras perarmatum (Young & Bird 1822)

Pl. 5, figs. 1–4

1822 *Ammonites perarmatus* Young & Bird, 1–3 May 1822[2] : 249; pl. 14, fig. 11 (*non Ammonites perarmatus* J. Sowerby, 1 June 1822)
1828 *Ammonites subarmatus* Young & Bird : 263; pl. 14, fig. 8.
1843 *Ammonites andraei* Simpson : 23.
1855 *Ammonites andraei* Simpson; Simpson : 59.
1912 *Porpoceras perarmatum* (Young & Bird) Buckman : pl. 50.
1912 *Porpoceras andraei* (Simpson) Buckman : pl. 57.
1963 *Peronoceras andraei* (Simpson); Sapunov : 128; pl. 6, fig. 4.

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[2] Evidence for the publication date of Young & Bird's *Geological Survey of the Yorkshire Coast* can be found in the *Monthly Magazine*, London, **53** (368) : 446, for 1 June 1822, where it was included in a review of books published during May 1822, and also in a paper by Young (1822, *Mem. Wernerian Soc.*, Edinburgh, 4 : 262) on the Kirkdale Caves, read to the Wernerian Natural History Society of Edinburgh on 4 May 1822, where he said that his book was 'just published'. The publication date was, therefore, 1, 2 or 3 May 1822, and *Ammonites perarmatus* Young & Bird has priority over *A. perarmatus* J. Sowerby published on 1 June 1822 (Sowerby 1822 : 72; pl. 352; for date of publication see Cleevely 1974 : 443), and now known to be an Oxfordian *Euaspidoceras* (Arkell 1940 : 193).

HOLOTYPE. Whitby Museum no. 180, figured by Buckman (1912 : pl. 50).

DIAGNOSIS. Whorl section varies between square and depressed. Ribs of low density and widely spaced throughout growth; though mainly single and bearing prominent ventrolateral tubercles, some are looped in pairs to the tubercles. Most ribs bifurcate at the tubercles, and secondaries are projected forwards and widely spaced on the venter.

DESCRIPTION. Specimens in which the primary ribs are considerably more widely spaced than in *P. fibulatum*, and in which the whorl section varies between square and much depressed, frequently accompany the more compressed and densely ribbed *P. fibulatum*. The holotype of *P. perarmatum* from Yorkshire is an extreme type, in which the whorl breadth is very large, the ribs are very widely spaced and there is only occasional fibulation on the inner whorls which have large ventrolateral tubercles. The venter is badly worn by erosion on most of the outer whorl as is shown in Buckman's figure (1912 : pl. 50). A less extreme Yorkshire specimen is figured here (Pl. 5, fig. 1) that has its ventral ribs intact. All gradations exist between this and the square-whorled type exemplified by the holotype of *Ammonites andraei* (Buckman 1912 : pl. 57). Regular fibulation in the latter specimen extends up to 40–50 mm diameter, after which the ribs are mainly single, with small to moderate ventrolateral tubercles.

In Northamptonshire *P. perarmatum* also has the same vertical range as *P. fibulatum*, for it occurs in the Unfossiliferous Beds and in the Lower and Middle *Leda ovum* Beds. A portion of an adult body chamber that has a much depressed whorl section is figured in Pl. 5, fig. 2, and although both ends of it are missing the whorl can be seen to become rapidly more compressed towards the aperture, which must have been at about 65 mm diameter. Another specimen with a less strongly depressed whorl section is figured in Pl. 5, fig. 4, and a nearly complete adult body chamber with a square whorl section in Pl. 5, fig. 3. The latter specimen shows an example of a constriction at a former mouth border followed by a further short period of growth (less than $\frac{1}{4}$ of a whorl), and it is interesting to note that the single ribs and ventrolateral tubercles after the first constriction bear great resemblance to those of *Zugodactylites*, and are considerably different from the widely-spaced fibulate ribs of the previous half whorl.

Genus *ZUGODACTYLITES* Buckman 1926

TYPE SPECIES. *Ammonites braunianus* d'Orbigny 1845.

SYNONYMY. *Omolonoceras* Dagis 1967 (type species: *O. manifestum*); *Gabillytes* Guex 1971 (type species: *G. larbusselensis*).

DIAGNOSIS. Characterized by single, straight primary ribs that bifurcate at small sharp ventrolateral tubercles, and form forwardly projected secondary ribs on the venter. Some single ribs occur on the adult body chamber. Whorl shape varies from compressed to depressed, and the

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Plate 4 ×1 (Fig. 4, ×1·5)

Peronoceras fibulatum (J. de C. Sowerby), Fibulatum Subzone

Fig. 1. Bed 62, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.56539.

Fig. 2. Top part of Unfossiliferous Beds, railway cutting 1·2 km south of Long Buckby, Northamptonshire; Northampton Museum, B. Thompson Colln.

Peronoceras turriculatum (Simpson), Fibulatum Subzone

Fig. 3. Unfossiliferous Beds, Hollowell, 13 km north-west of Northampton; Northampton Museum, B. Thompson Colln.

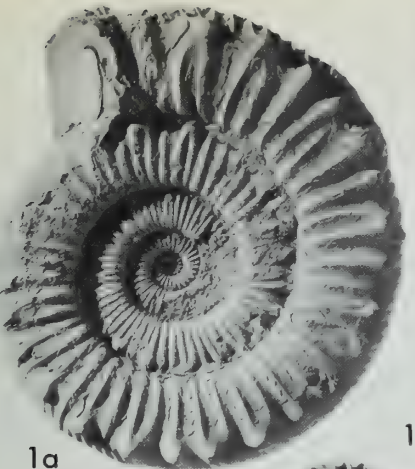
Fig. 6. Lower or Middle *Leda ovum* Beds, Badby, 3 km south of Daventry, Northamptonshire; Northampton Museum, B. Thompson Colln.

Fig. 8. Middle *Leda ovum* Beds, Eydon, Northamptonshire; OUM J.20138*a*, E. A. Walford Colln.

Peronoceras subarmatum (Young & Bird), Fibulatum Subzone

Figs 4, 7. [? Lower] *Leda ovum* Beds, Bugbrooke, Northamptonshire; Miss A. E. Baker Colln. Fig. 4, BM 20843, ×1·5. Fig. 7, BM 20135.

Fig. 5. Middle *Leda ovum* Beds, Eydon, Northamptonshire; OUM J.20146, ? E. A. Walford Colln.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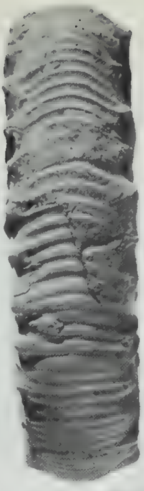
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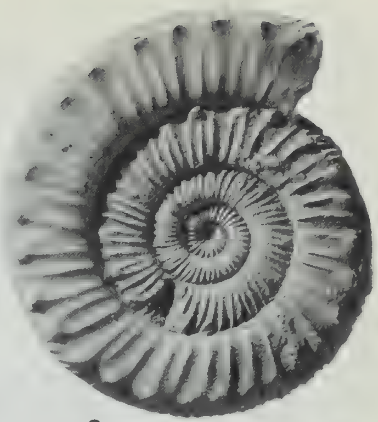
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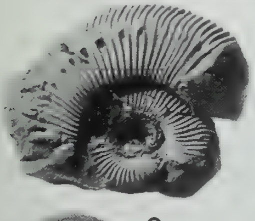
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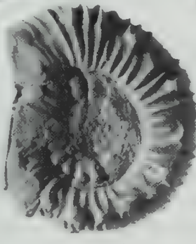
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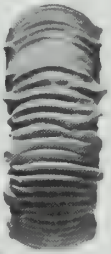
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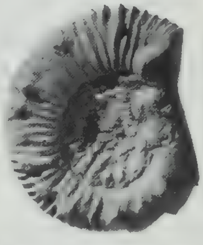
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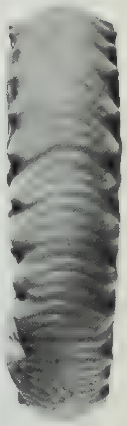
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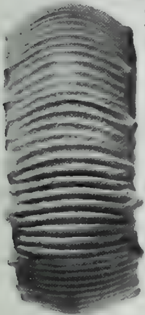
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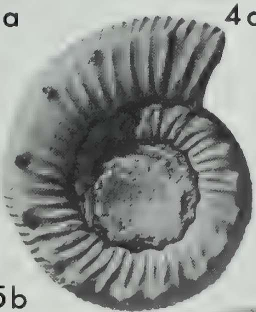
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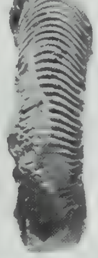
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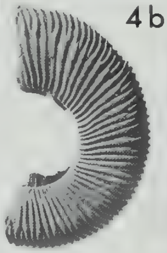
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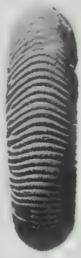
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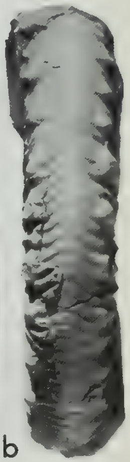
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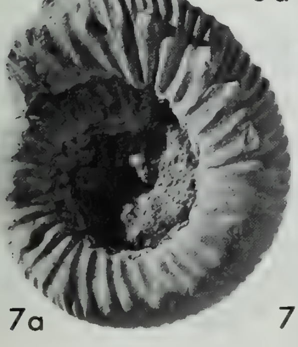
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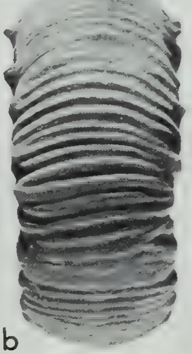
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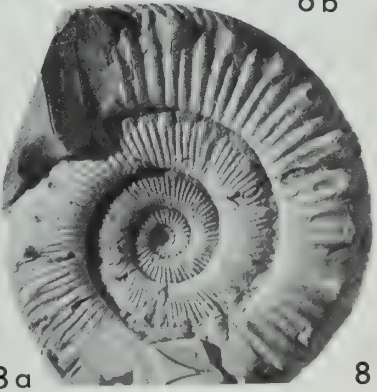
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depressed whorls may be coronate with large ventrolateral tubercles. A blunt ventral keel is formed in one species. Complete adults have a strong constriction immediately before the adult mouth border.

DISTRIBUTION. Fibulatum Subzone, lower (but not basal) and middle parts. Northamptonshire: Lower and Middle *Leda ovum* Beds. Yorkshire: Whitby beds 62–64, Ravenscar bed xxxi.

REMARKS. The sharp ventrolateral tubercles that occur at the ends of all the primary ribs are characteristic of all species of *Zugodactylites*. In this respect they differ from the accompanying species of *Peronoceras* which have fibulate ribs. The most likely ancestor for *Zugodactylites*, the fine-ribbed species *Peronoceras turriculatum*, always has some fibulate ribs. Like *Peronoceras*, *Zugodactylites* shows a wide range of whorl shapes occurring in the same bed. The compressed- and depressed-whorled forms remain considerably different up to the end of the adult body chamber, so they are considered to be specifically distinct. They do not change to much more similar morphology on the body chamber, as was found in species of *Orthodactylites* in the Tenuicostatum Zone (Howarth 1973), where the depressed and compressed forms were considered to be conspecific. *Zugodactylites* with complete adult body chambers are, in fact, remarkably frequent, and although the rib-density shows wide variation, there is much less variation in final size, and species are fairly closely defined.

The variation in whorl shape in *Zugodactylites* led Dagis (in Dagis & Dagis 1967) to propose the generic name *Omolonoceras* for those forms with depressed whorls. Dagis (1968 : 52–56, 73, 84) showed that these depressed forms occur in north-eastern Siberia in the same beds as *Zugodactylites*. The difference in whorl shape is not considered here to be worthy of generic distinction, because compressed and depressed forms of Dactylioceratidae that are clearly related by other distinctive characters often occur together in the same bed, and in some cases (*Orthodactylites* of the Tenuicostatum Zone) they may even be conspecific. *Omolonoceras* has the same sharp ventrolateral tubercles on single ribs that are the main characteristic of *Zugodactylites*.

Generic distinction of a different sort was put forward by Guex (1971) when he proposed the name *Gabillytes* for the small keeled species *Zugodactylites pseudobraunianus* (Monestier) (*G. larbusselensis* is a synonym). Sexual dimorphism was the real basis claimed for the proposal of the genus. If *Z. pseudobraunianus* and *Z. braunianus* could be shown to be sexual dimorphs, then they should be referred to the same species, rather than made generically different. However, *Z. pseudobraunianus* is much less common than *Z. braunianus* in England and it has not been found at all in Yorkshire. The ventral keel occurs most prominently on the last whorl of the phragmocone before the adult body chamber, and is lost on the adult. Such a prominent keel is not found in *Z. braunianus* at any growth stage, although the venter may be raised in some individuals at much larger sizes into a pseudo-keel. So the keel of *Z. pseudobraunianus* is a morphological feature that is not associated with the adult body chamber. The case for dimorphism seems to be unproved, and the two forms are here kept as different species.

Plate 5 ×1

Peronoceras perarmatum (Young & Bird), Fibulatum Subzone

Fig. 1. Beds 60–63, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.76486.

Fig. 2. *Leda ovum* Beds, railway cutting, Eydon, Northamptonshire; OUM J.20139, E. A. Walford Colln.

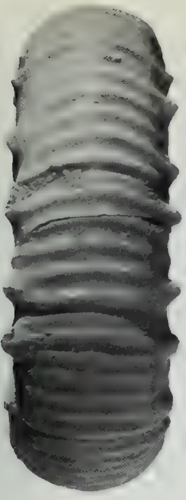
Fig. 3. *Leda ovum* Beds, Northampton; BM C.67507.

Fig. 4. Lower *Leda ovum* Beds, Thenford Hill, 7 km north-east of Banbury, Northamptonshire; OUM J.20199.

Zugodactylites braunianus (d'Orbigny), Fibulatum Subzone

Fig. 5. Le Clapier, Aveyron, France; lectotype, Inst. Pal. Mus. Hist. Nat. Paris, d'Orbigny Colln. no. 1936.

Fig. 6. *Leda ovum* Beds, Northampton; OUM J.16288, C. Upton Colln.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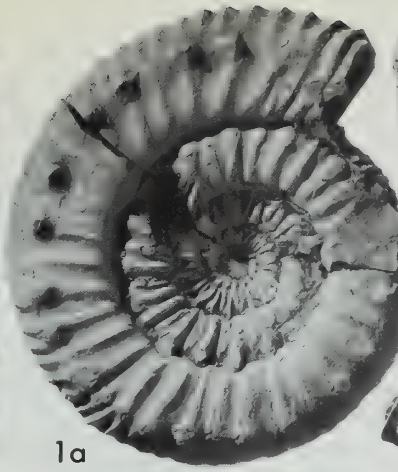
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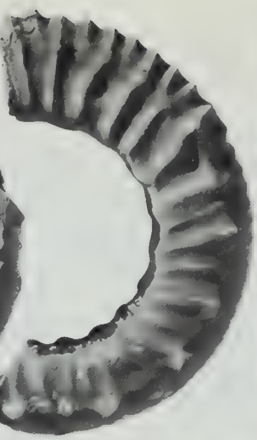
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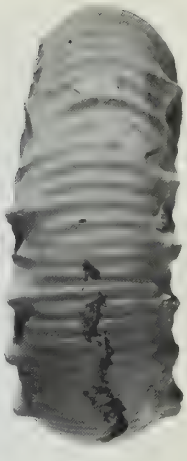
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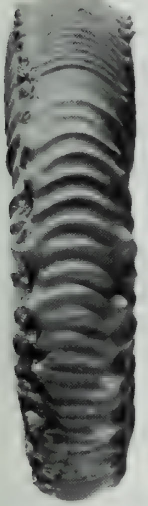
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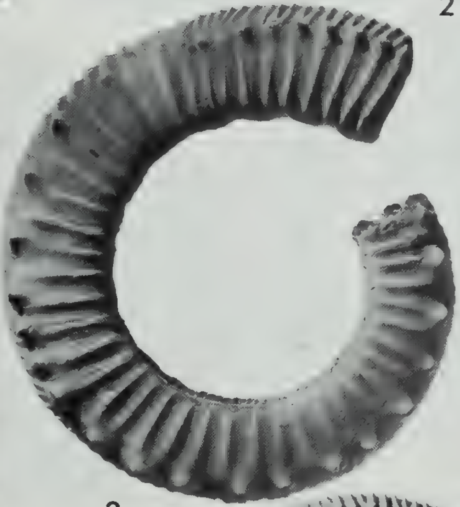
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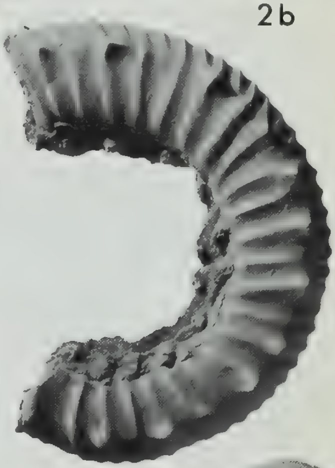
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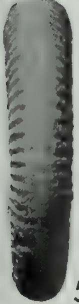
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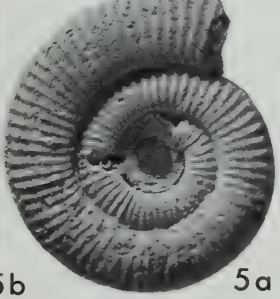
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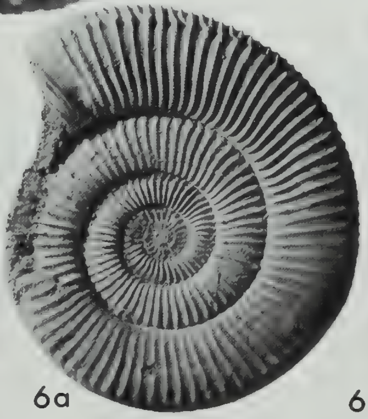
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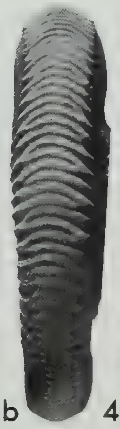
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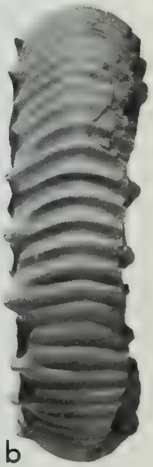
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Zugodactylites braunianus (d'Orbigny 1845)

Pl. 5, figs 5, 6; Pl. 6, figs 1–6; Pl. 7, figs 1–4; Pl. 8, fig. 5

1845 *Ammonites braunianus* d'Orbigny : 327; pl. 104, figs 1–3.
1874 *Ammonites braunianus* d'Orbigny; Dumortier : 103; pl. 28, fig. 5.
1885 *Ammonites braunianus* d'Orbigny; Quenstedt : 373; pl. 46, fig. 18.
1926 *Zugodactylites braunianus* (d'Orbigny) Buckman : pl. 658.
1927 *Zugodactylites braunianus* (d'Orbigny); Buckman : 44.
1927 *Zugodactylites mutatus* Buckman : pl. 720.
1931 *Coeloceras* (*Dactylioceras*) *braunianum* (d'Orbigny) Monestier : 53; pl. 3, figs 10, 13–19, 24.
1959 *Coeloceras* (*Dactylioceras*) *braunianum* (d'Orbigny); Théobald & Duc : 21; pl. 2, figs 9, 9*a*.
1961 *Zugodactylites braunianus* (d'Orbigny); Dean, Donovan & Howarth : pl. 73, fig. 1.
? 1966 *Zugodactylites braunianus* (d'Orbigny); Fischer : 43; pl. 2, fig. 6; pl. 5, fig. 9.
1966 *Zugodactylites sapunovi* Géczy : 440; pl. 1, fig. 3.
1967 *Zugodactylites moratus* Dagis : 63; pl. 1, figs 3, 4.
1968 *Zugodactylites braunianus* (d'Orbigny); Dagis : 41; pl. 8, figs 4–6.
1968 *Zugodactylites moratus* Dagis; Dagis : 49; pl. 8, figs 7, 8.
1970*a* *Zugodactylites braunianus* (d'Orbigny); Guex : 342; pl. 1, fig. 2.
1970*b* *Zugodactylites braunianus* (d'Orbigny); Guex : 623; pl. 1, figs 1–7.
1973*b* *Zugodactylites braunianus* (d'Orbigny); Guex : 552; pl. 3, figs 10, 11.
1975 *Zugodactylites* cf. *braunianus* (d'Orbigny); Frebold : 15; pl. 5, figs 3–5, ? 6.

LECTOTYPE. The best specimen in d'Orbigny's collection (Inst. Pal., Mus. Hist. Nat. Paris) is no. 1936 from Le Clapier, Aveyron, and is here designated lectotype (Pl. 5, fig. 7 – it was figured previously by Guex 1970*b* : pl. 1, figs 5–7). It is the largest of the syntypes on which d'Orbigny based his description, and the specimen from which he obtained his measurements (his value of 0·12 for the whorl thickness is evidently an error, and his figure of a 58 mm diameter specimen, said to be natural size, is either idealized or enlarged). Dimensions (mm) of the lectotype are – 43·0: 10·6 (0·24), 9·5 (0·22), 22·8 (0·53).

DIAGNOSIS. A finely-ribbed, compressed species of *Zugodactylites*. The whorl height exceeds the whorl breadth at sizes of more than about 20 mm diameter. The whorl section is rounded, with a rounded or arched venter. The ribs are generally fine, but show wide variation in density; they are straight and bifurcate at small sharp ventrolateral tubercles; the secondary ribs are arched forwards on the venter, and are sometimes raised and sharp in the middle of the venter. Maximum size of complete adults varies between 43 and 90 mm diameter, and a strong constriction occurs immediately before the mouth border.

DISTRIBUTION. Fibulatum Subzone. Lower and Middle *Leda ovum* Beds of Northamptonshire; beds 62–64 at Whitby, and bed xxxi at Ravenscar, Yorkshire.

DESCRIPTION. About 60 solid and well-preserved specimens from the *Leda ovum* Beds of the Northampton area have been examined; most of the best specimens came from the former brickpits, especially Vigo brickpit, which were within the town itself. In addition many crushed and fragmentary specimens occur in the cores of the numerous boreholes that have penetrated that clay formation. Of the 30 specimens that belong to Beeby Thompson's collection, 23 came from the Lower *Leda ovum* Beds and 7 from the Middle *Leda ovum* Beds, and the species is not known from lower or higher horizons. About half the specimens are complete adults, each with a deep constriction immediately before the mouth border. The constriction affects both inside and

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Plate 6 ×1

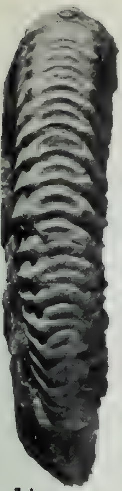
Zugodactylites braunianus (d'Orbigny), Fibulatum Subzone

Figs 1, 3, 5. Lower *Leda ovum* Beds, Heyford, 10·5 km west of Northampton. Fig. 1, BM C.67525. Fig. 3, BM C.67524. Fig. 5, BM C.56068.

Fig. 2. Lower or Middle *Leda ovum* Beds, Vigo brickpit, Northampton; Northampton Museum, B. Thompson Colln.

Fig. 4. Lower or Middle *Leda ovum* Beds, Northampton; BM C.67521.

Fig. 6. Middle *Leda ovum* Beds, Racecourse brickpit, Northampton; BM C.67533.



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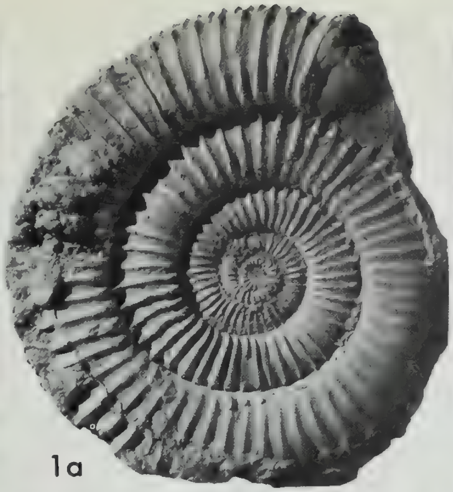

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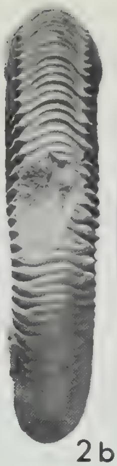

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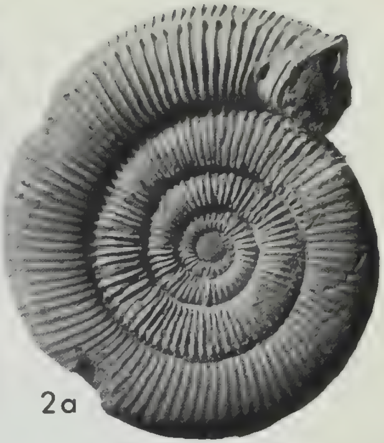

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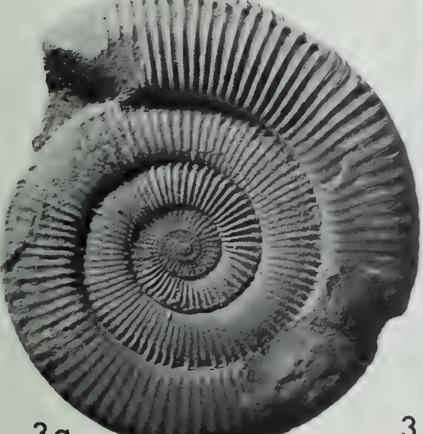

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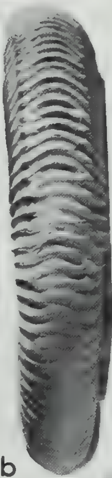

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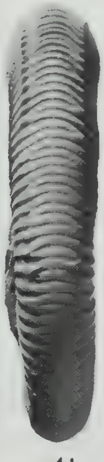

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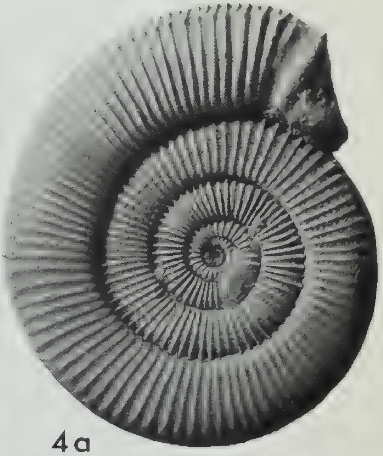

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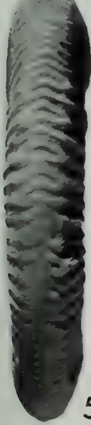

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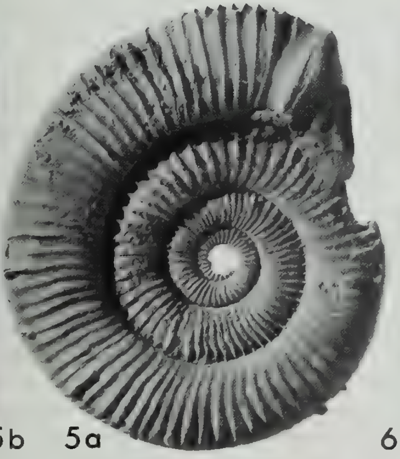

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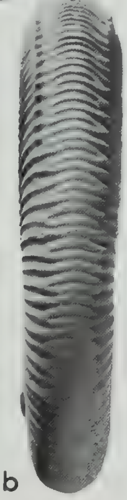

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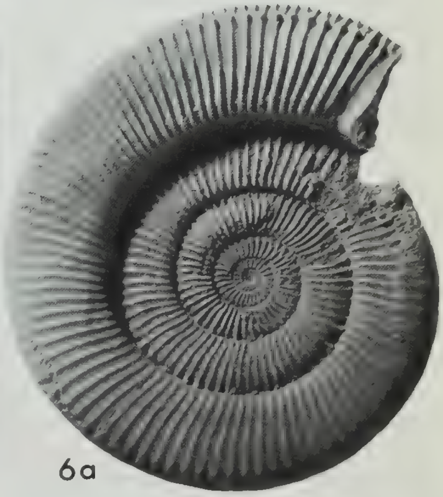


6a

outside surfaces of the shell, in it the ribs are much reduced or absent, and it is followed by one or two swollen ribs before the mouth border itself. Such constrictions can be seen in all the specimens figured here, and in the one figured by Buckman (1927 : pl. 720); none of them have constrictions before the final mouth border. In 31 specimens the diameter at the adult mouth border varies between 43 and 70 mm; the mean value (M) is 57·8 mm, the standard deviation (s) is 7·0 mm and the range spanned by M ± 2s is 43·8–71·8 mm. The histogram (Fig. 3) confirms that the distribution is unimodal with a peak frequency between 55 and 60 mm. Similarly the diameter at the last suture-line in 23 adult specimens varies between 31 and 47·5 mm, the mean being 39·2 mm and the standard deviation 4·5 mm. The length of the adult body chamber in 22 adults varies between $\frac{11}{16}$ and $\frac{15}{16}$ whorl, the mean being $\frac{13}{16}$ whorl.

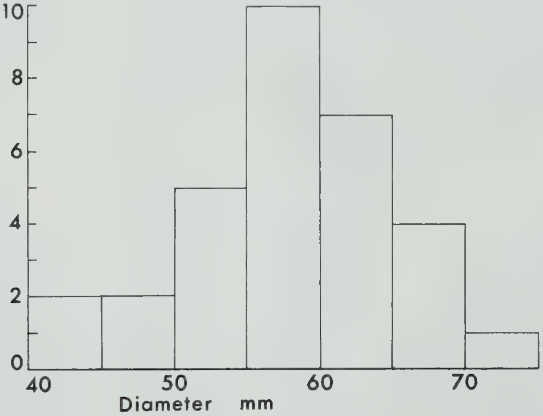


Fig. 3. Histogram of the diameter at the mouth border of 31 specimens of *Zugodactylites braunianus* from Northamptonshire.

Z. braunianus has compressed whorls, and in the Northampton population it can be seen (Fig. 4) that the height of the whorl always exceeds the breadth at sizes of more than 6 mm whorl height (*c*20 mm diameter). On the largest whorls the height/breadth ratio may reach 1·4. There is wide variation in rib-density, and the full range can be seen in the series of specimens figured in Pl. 5, fig. 6, Pl. 6, figs 1–3, 5, 6, Pl. 7, fig. 1 and in Dean, Donovan & Howarth (1961 : pl. 73, fig. 1). These eight form a continuously grading series, though the end-members, Pl. 6, figs 1 and 3, look considerably different. The rib-density of the 48 measurable specimens is expressed graphically in Fig. 5A, and that of the eight figured specimens in Fig. 5C. These are conventional graphs, in which the number of ribs in a complete whorl is plotted against the diameter of that whorl at its larger end. Close inspection of the ribbing reveals many instances of uneven rib spacing over short lengths of a whorl, so in order to express the changes in rib-density more accurately, 90° quadrants were marked on the specimens and counts of the number of ribs per quarter whorl were made. The relatively high rib-density of the species allows this to be done without appreciable errors. Graphs can now be plotted of the number of ribs in a quarter of a whorl against the whorl diameter at its larger end. The results are shown in Fig. 5B for the 48 Northamptonshire specimens and Fig. 5D for the eight figured specimens. The general unevenness of the ribbing is much more clearly displayed, and the rib-curves of the eight figured specimens are interlaced to such an extent that the apparent separation of the rib-curves in the ribs per whorl graph (Fig. 5B) is seen to be largely spurious. The wide range of variation observed in rib-density appears to be a genuine character of the species, and not due to the mixing of specimens from different horizons, because specimens of widely differing rib-densities occur in both the Lower and the Middle *Leda ovum* Beds; e.g. four of the specimens in Figs 5C and 5D (nos 3, 5, 6, 8), including the most densely and the most coarsely ribbed individuals, came from the Heyford brickpit, where only the Lower *Leda ovum* Beds were exposed, whilst the densely ribbed specimen from the

Racecourse brickpit, Northampton, and the coarsely ribbed Abington Park sewer trench specimen (Figs 5C, 5D, nos 2 and 7) both came from the Middle *Leda ovum* Beds. A graph of the rib-density of the Vigo specimens alone occupies 90% of the variation shown by the whole fauna. The Vigo specimen figured by Buckman (1927 : pl. 720) as the holotype of *Zugodactylites mutatus* is a typical *Z. braunianus* in all respects.

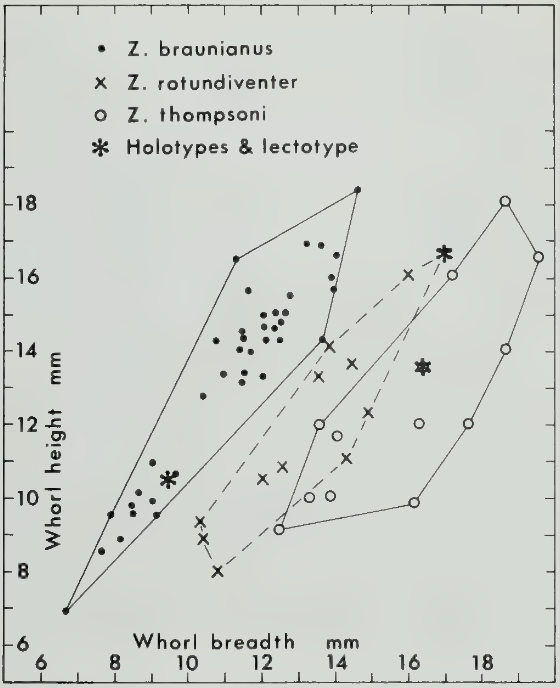


Fig. 4. Graph of whorl height plotted against whorl breadth for 35 specimens of *Zugodactylites braunianus* from Northamptonshire and four from Yorkshire, nine specimens of *Z. rotundiventer* from Northamptonshire, and eight specimens of *Z. thompsoni* from Northamptonshire and one from Yorkshire.

Examples of *Zugodactylites* have now been found in the lower and middle part of the Fibulatum Subzone of the Yorkshire coast (see p. 243). Six specimens are known from beds 62–64 of the main outcrop at Whitby, and 17 specimens were obtained from bed xxxi at Ravenscar. The Whitby examples include the large complete specimen figured in Pl. 7, fig. 3, whilst those from Ravenscar include those figured in Pl. 8, fig. 5, which is an exact match for the Northamptonshire specimen figured by Dean, Donovan & Howarth (1961 : pl. 73, fig. 1), Pl. 7, fig. 2, which has thicker whorls than average and is transitional to *Z. rotundiventer*, and Pl. 7, fig. 4, which is the most densely ribbed Yorkshire specimen. Although the Yorkshire population is morphologically close to that of Northamptonshire and the two are clearly conspecific, there are some differences. The main one is the larger sizes attained by the Yorkshire adult specimens: nine complete adults ranged from 61 to 86 mm in diameter at the mouth border, the mean being 73·8 mm and the standard deviation 7·3 mm; this larger size probably reflects the more advantageous ecological conditions in which the Yorkshire population lived. The only other significant difference is in the rib-density: the Yorkshire specimens all fall in the lower two-thirds of the range of variation of the Northampton specimens shown in Fig. 5A.

The ventrolateral tubercles are small and sharp when seen on the outer surface of the main shell or as moulds of the inner surface of the main shell, but the 'inner shell' (Howarth 1975) cuts across the base of the tubercles, so that they are hardly visible on the surface of the inner shell or

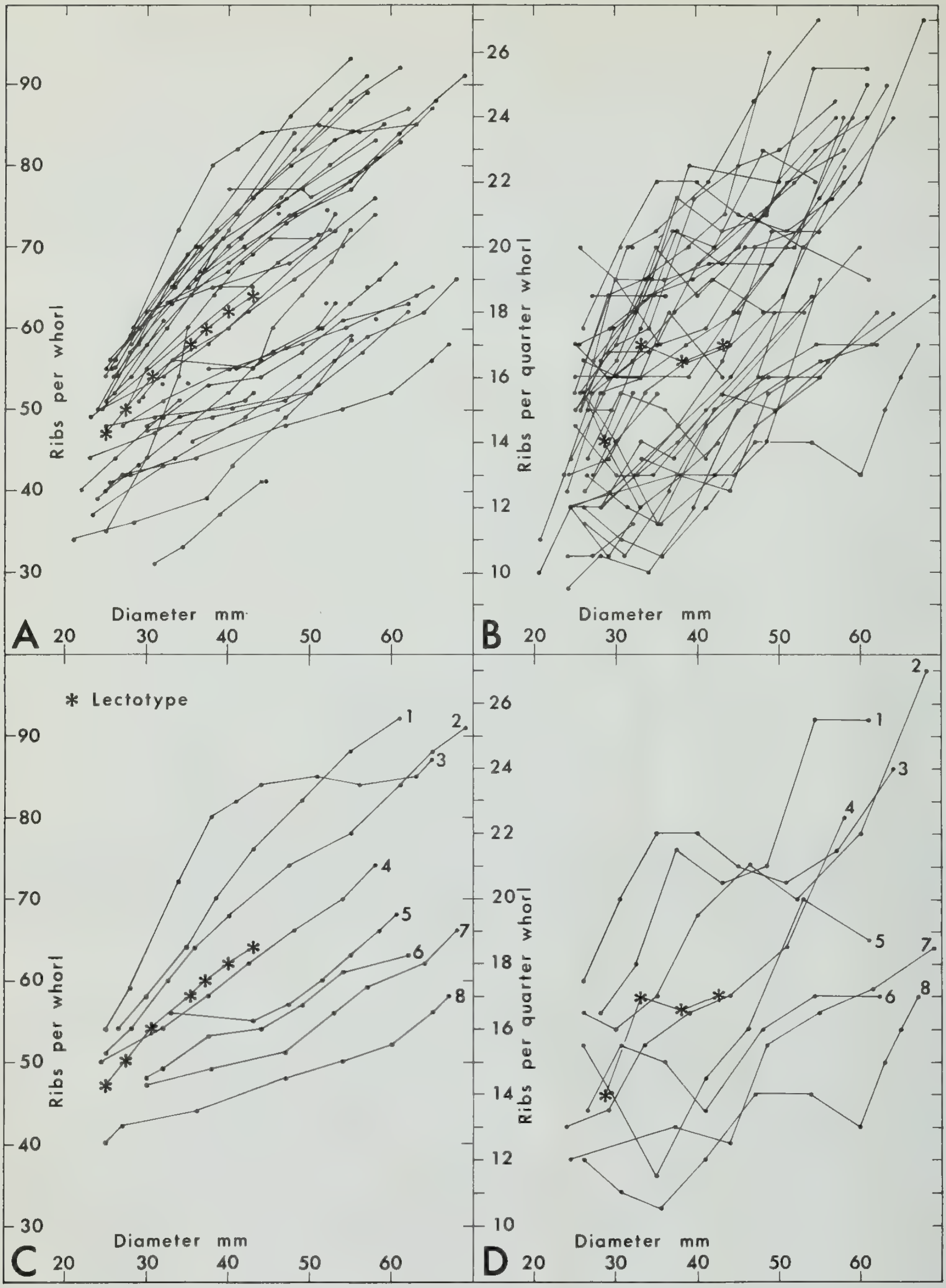


Fig. 5. Graphs of rib-density of *Zugodactylites braunianus*. Figs 5A and 5B each contain about 225 points obtained from 48 specimens from Northamptonshire. Figs 5C and 5D are plots of eight specimens selected to show almost the full range of rib-density. 1 = Northampton Museum specimen, Pl. 6, fig. 2; 2 = BM C.67533, Pl. 6, fig. 6; 3 = BM C.67524, Pl. 6, fig. 3; 4 = OUM J.16288, Pl. 5, fig. 6; 5 = BM C.56068, Pl. 6, fig. 5; 6 = BM C.56067, figured Dean, Donovan & Howarth 1961 : pl. 73, fig. 1; 7 = Northampton Museum, Pl. 7, fig. 1; 8 = BM C67525, Pl. 6, fig. 1.

on the internal mould. Some ribs bifurcate while others remain single at the ventrolateral tubercles, and the proportion of ventral to primary ribs is about 1·5 in many specimens, but varies between 1·3 and 1·8 and is independent of the variations in rib-density. The ventral ribs sometimes zigzag across the venter between tubercles that are not opposite each other on the sides of the venter. In some specimens the middle of the venter is slightly raised into a pseudo-keel, and the secondary ribs across it are raised and sharp in the middle, accentuating the effect.

The lectotype, from Le Clapier, Aveyron, was previously figured by Guex (1970*b* : pl. 1, figs 5–7). In whorl height and breadth, and in rib-density, it occupies a position in the centre of the variation of the Northamptonshire population (Figs 4 and 5). Guex's (1970*b* : 625) opinion, that the specimen figured by Dean, Donovan & Howarth (1961 : pl. 73, fig. 1) (Fig. 5C, no. 6) differed significantly from the lectotype and might have come from a different horizon, is not borne out by the analysis given here, for both are well within the ranges of variation of both the Northamptonshire and Yorkshire specimens, the latter being known to have come from a more restricted horizon. Other Aveyron specimens were figured by Dumortier, Monestier, Theobald & Duc and Guex as listed in the synonymy. Dumortier's (1874 : 103, pl. 28, fig. 5) specimens of 90 and 99 mm diameter are bigger than many English specimens, but they agree closely otherwise, and Monestier's (1931 : 53) specimens appear to be rather more compressed, but further specimens and analysis are needed before convincing differences could be established.

A single specimen from the manganese mine of Urkut, Hungary, was made the type of the new species *Z. sapunovi* by Géczy (1966 : 440) because it had partly bifurcating ribs and a raised pseudo-keeled venter. Partly bifurcating ribs with a secondary/primary ratio of between 1·3 and 1·8 are typical of *Z. braunianus*, and a raised venter with a pseudo-keel occurs in about one-third of the Northamptonshire collection (Pl. 6, fig. 5 shows the feature well). Many of them have a cross-section like that given by Géczy, whose specimen is a *Z. braunianus*, probably adult at about 70 mm diameter and with about 100 ribs on the final whorl. The specimens described by Dagis (1968 : 41) from north-eastern Siberia are also very similar to the Northamptonshire fauna. They include the new species *Z. moratus* Dagis (1968 : 49) which was used for those examples with a slightly greater whorl breadth. They are not as broad as *Z. rotundiventer*, and they are best accommodated in *Z. braunianus*, of which they appear to be slightly broader-whorled immature examples.

Zugodactylites rotundiventer Buckman 1927

Pl. 7, figs 5, 6

1927 *Zugodactylites rotundiventer* Buckman : pl. 743.
1966 *Zugodactylites rotudiventer* Buckman; Fischer : 44; pl. 2, fig. 17; pl. 5, fig. 8.
1967 *Zugodactylites latus* Dagis : 65; pl. 1, fig. 5.
1968 *Zugodactylites latus* Dagis; Dagis : 51; pl. 8, fig. 9.

HOLOTYPE. BM C.71443 (Buckman 1927 : pl. 743) from the *Leda ovum* Beds at Vigo brickpit, Northampton. Dimensions (mm) – 73·5: 16·7 (0·23), 17·0 (0·23), 42·5 (0·58).

DIAGNOSIS. Differs from *Z. braunianus* in the larger whorl breadth, which equals or exceeds the whorl height at all growth stages. Ribbing similar to *Z. braunianus*, with small sharply-pointed ventrolateral tubercles.

DISTRIBUTION. Fibulatum Subzone, Lower *Leda ovum* Beds of Northamptonshire.

DESCRIPTION. The collection consists of the holotype and eight other specimens, all from the *Leda ovum* Beds of Northamptonshire. One is from Heyford brickpit, 10 km west of Northampton, while the remainder are from Vigo brickpit, and six of them were labelled by Beeby Thompson as coming from the Lower *Leda ovum* Beds. Unfortunately the holotype was not so labelled, but there is no evidence that it or any others came from a horizon other than the Lower *Leda ovum* Beds. The species has a broad arched venter at all sizes, and a considerably larger whorl breadth than *Z. braunianus* (Fig. 4). At diameters of 40 mm and larger the whorl height and breadth may be approximately equal, but at smaller sizes the whorl breadth always exceeds the height. The primary ribs, sharp ventrolateral tubercles and secondary ribs on the venter are similar to those in *Z.*

braunianus, and the rib-density is the same as the lower half of the range of variation in *Z. braunianus*. The primary ribs bifurcate or remain single at the ventrolateral tubercles, and the ratio of secondary/primary ribs is about 1·5.

Four of the specimens are adults. The holotype has a constriction immediately preceding a flared mouth border at 75 mm diameter; its body chamber occupies exactly one whorl, but only small parts of the final suture-lines can be seen. A second, fragmentary specimen has a similar constriction and mouth border at 65 mm diameter and the body chamber occupies slightly more than one whorl. Two much smaller specimens (Pl. 7, figs 5, 6) have constrictions and mouth borders at 34 and 35 mm diameter preceded by $\frac{7}{8}$ and $\frac{13}{16}$ whorl of body chamber respectively and crowded final suture-lines in both cases.

Dagis (1968 : 51) referred specimens with the same whorl height/breadth ratio and the same rib-density as the Northamptonshire specimens to his new species *Z. latus*, which appears to be a synonym.

Zugodactylites thompsoni sp. nov.

Pl. 8, figs 1–4

HOLOTYPE. BM C.67529 from the Lower *Leda ovum* Beds at Heyford brickpit, Northamptonshire. Dimensions (mm) – 48·5: 13·6 (0·28), 16·4 (0·34), 24·3 (0·50).

PARATYPES. BM C.79468 from Hollowell, Northamptonshire; OUM J.20213 from Eydon, Northamptonshire; four specimens in Northampton Museum, three of them from Vigo brickpit and one from Greenough's brickpit, Northampton; one specimen from Vigo brickpit in the collections of the Northamptonshire Natural History Society and Field Club; BM C.68503 from bed xxxi at Ravenscar, Yorkshire.

DIAGNOSIS. A cadicone species of *Zugodactylites*, in which the whorl breadth exceeds the whorl height at all growth stages. The venter is wide and arched especially at sizes below 50 mm diameter. Ribs on the inner whorls are widely spaced, and each bears a moderate to large ventrolateral tubercle, giving a coronate whorl shape.

DISTRIBUTION. Fibulatum Subzone. Lower and Middle *Leda ovum* Beds of Northamptonshire, and bed xxxi at Ravenscar, Yorkshire.

DESCRIPTION. The holotype (Pl. 8, fig. 1) and seven of the paratypes of this species come from the *Leda ovum* Beds of Northamptonshire. Four of the paratypes are in Beeby Thompson's collection: two were definitely found in the Lower *Leda ovum* Beds, while one came from the Middle *Leda ovum* Beds, so that its stratigraphical range is the same as that of *Z. braunianus*. The specimen figured in Pl. 8, fig. 4 is a complete adult with a mouth border at 47 mm diameter preceded by a strong constriction, and its body chamber is $\frac{7}{8}$ whorl long. The largest paratype (Pl. 8, fig. 3) is incomplete at its aperture at 65 mm diameter, but there are indications that it was an adult and about 75 mm in diameter when complete up to its mouth border. The holotype and most of the other Northamptonshire paratypes have adult, but incomplete, body chambers, and they would all have been between 45 and 70 mm in diameter when complete.

Plate 7 ×1

Zugodactylites braunianus (d'Orbigny), Fibulatum Subzone

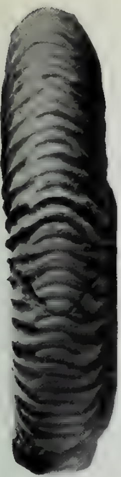
Fig. 1. Middle *Leda ovum* Beds, sewer trench, Abington Park, Northampton; Northampton Museum, B. Thompson Colln.

Figs 2, 4. Bed xxxi, Alum Shales, foreshore below Ravenscar, Yorkshire. Fig. 2, BM C.78232. Fig. 4, BM C.78234.

Fig. 3. Bed 63, 0·30 m (1 ft) below top, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.78205.

Zugodactylites rotundiventer Buckman, Fibulatum Subzone

Figs 5, 6. Lower *Leda ovum* Beds, Vigo brickpit, Northampton. Fig. 5, BM C.79467. Fig. 6, BM C.79466.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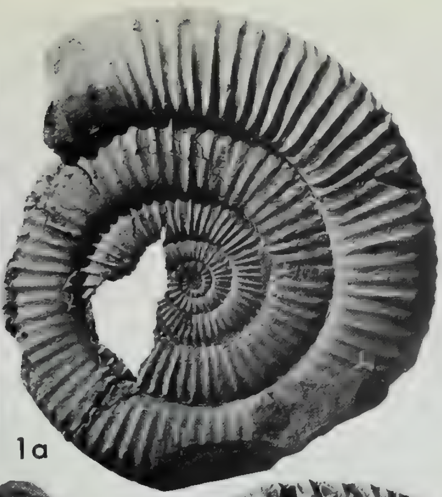
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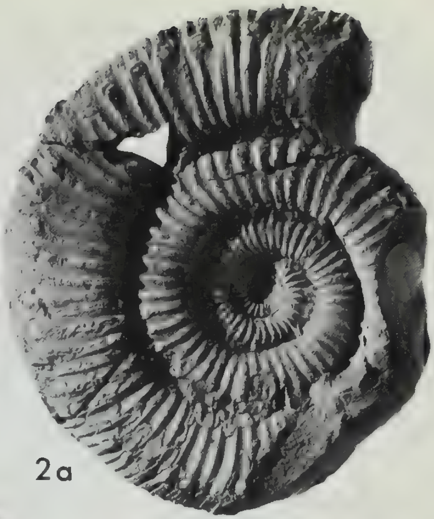
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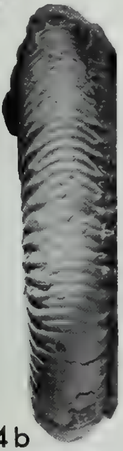
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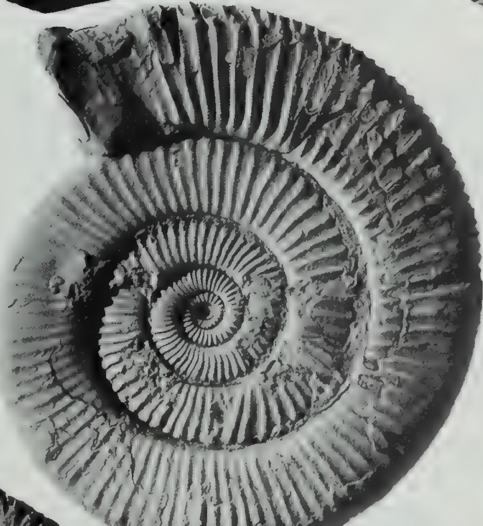
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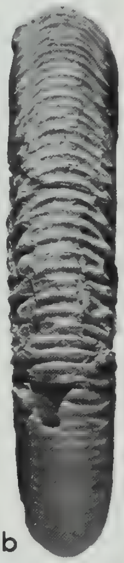
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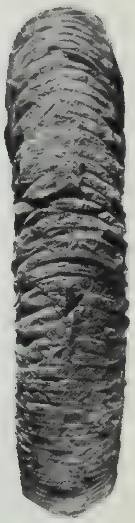
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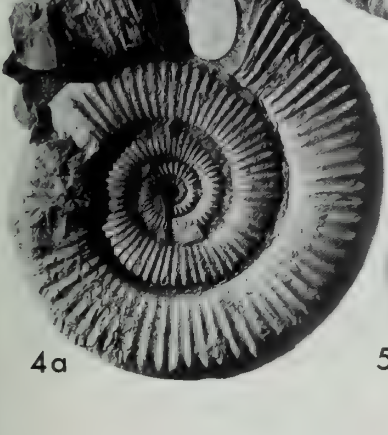
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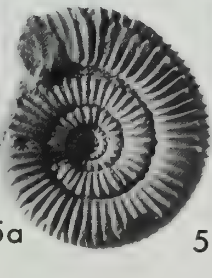
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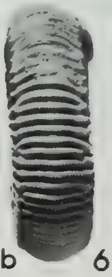
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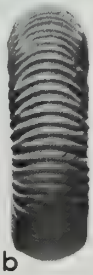
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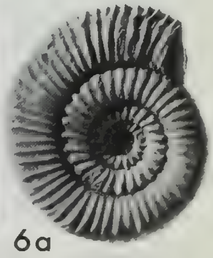
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The single Yorkshire specimen (Pl. 8, fig. 2) is from bed xxxi at Ravenscar where *Z. braunianus* also occurs commonly. It is probably an adult but the final part of the body chamber and the mouth border are missing. The body chamber preserved is $\frac{3}{4}$ whorl long and ends at 61 mm diameter; when complete with a body chamber one whorl long, it would have been about 70 mm in diameter. The ribs are rather more widely spaced throughout than in the holotype, and the large ventrolateral tubercles on the inner whorls become considerably smaller on the outer whorl.

The main distinguishing feature from *Z. braunianus* and *Z. rotundiventer* is the whorl shape, which is always depressed, with the whorl breadth exceeding the height, but there is considerable variation depending on the growth stage reached (Fig. 4). Another difference is the development of moderate to large ventrolateral tubercles on whorls up to about 35 mm diameter, which diminish in size at larger diameters to become not much larger than those in the other two species. The ribs generally bifurcate at the ventrolateral tubercles except on the final part of the adult body chamber where some single ribs occur (Pl. 8, fig. 3).

This is the only species of *Zugodactylites* in England that has a much depressed whorl shape and large ventrolateral tubercles on the inner whorls. The only other species of *Zugodactylites* with such depressed whorls are those from north-eastern Siberia described by Dagis (1967 : 48; 1968 : 52) as two species of his new genus *Omolonoceras*. Both have whorls similar in shape to those of *Z. thompsoni*, but they differ in having considerably smaller ventrolateral tubercles.

Zugodactylites pseudobraunianus (Monestier 1931)

Pl. 9, figs 4–7

1931 *Coeloceras* (*Dactylioceras*) *pseudobraunianum* Monestier : 54; pl. 3, figs 2, 4, ? 6, 7; pl. 9, fig. 15.
1971 *Gabillytes larbusselensis* Guex : 234, 239; pl. 2, figs 2a–d; pl. 3, fig. 3.
1972 *Gabillytes larbusselensis* Guex; Guex : pl. 8, figs 1, 2.
1973*b* *Gabillytes larbusselensis* Guex; Guex : 551; pl. 3, figs 9, 12–14.

LECTOTYPE. Monestier had three syntypes and one doubtful example. The largest figured syntype (Monestier 1931 : pl. 3, fig. 4; pl. 9, fig. 15) is here designated lectotype; it is from Guilhomard, Aveyron.

DIAGNOSIS. A small species of *Zugodactylites*, in which complete adults are 22–30 mm in diameter at the mouth border. The venter of whorls up to 18–20 mm diameter has a blunt keel, which is progressively lost on the final half whorl of the adult body chamber. Ribs fine and dense, bifurcating at small ventrolateral tubercles, and generally similar to the ribs in *Z. braunianus* at similar sizes.

DISTRIBUTION. Fibulatum Subzone. Lower *Leda ovum* Beds in Northamptonshire.

DESCRIPTION. The collection consists of 10 almost complete specimens and fragments of 15 further specimens from the Lower *Leda ovum* Beds at Vigo brickpit, Northampton. The largest example (Pl. 9, fig. 5) is 25 mm in diameter at its broken aperture, and it has $\frac{11}{16}$ whorl of body chamber with the last suture-lines (which are not approximated) at 16·5 mm diameter. It appears

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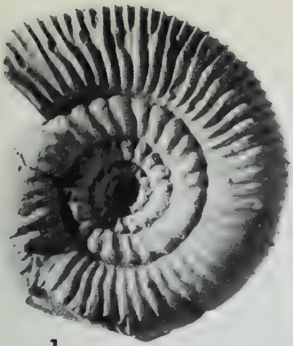
Plate 8 ×1

Zugodactylites thompsoni sp. nov., Fibulatum Subzone
Fig. 1. Lower *Leda ovum* Beds, Heyford, Northamptonshire; holotype, BM C.67529.
Fig. 2. Bed xxxi, Alum Shales, foreshore below Ravenscar, Yorkshire; BM C.68503.
Fig. 3. Middle *Leda ovum* Beds, Eydon, Northamptonshire; OUM J.20213.
Fig. 4. *Leda ovum* Beds, Hollowell, 13 km north-west of Northampton; BM C.79468.

Zugodactylites braunianus (d'Orbigny), Fibulatum Subzone
Fig. 5. Bed xxxi, Alum Shales, foreshore below Ravenscar, Yorkshire; BM C.78246.

Catacoeloceras crassum (Young & Bird), Crassum Subzone
Fig. 6. [? Upper] *Leda ovum* Beds, [? Nevill Holt area, Medbourne], Leicestershire; GSM 22519, Lady Exeter Colln. (collected pre-1865) (see p. 246).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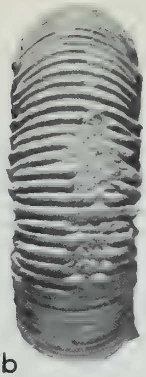
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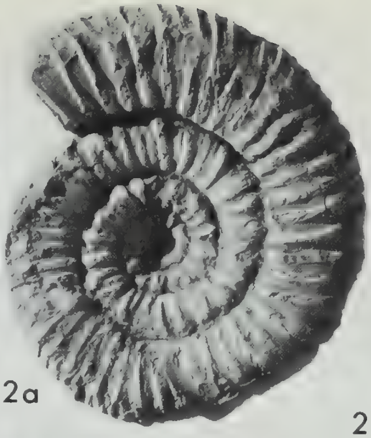
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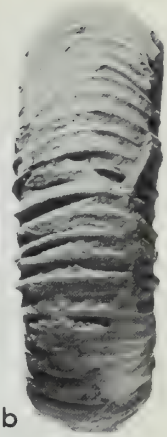
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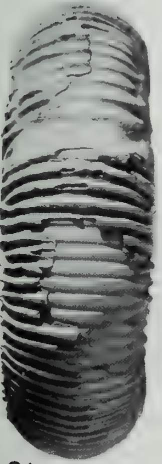
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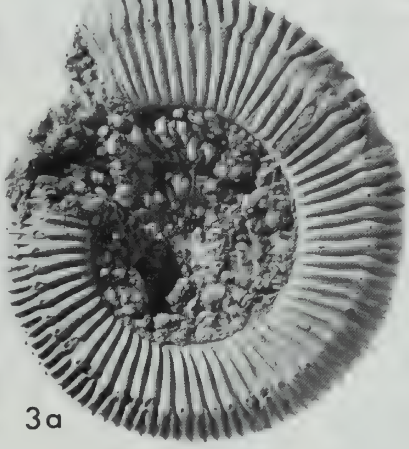
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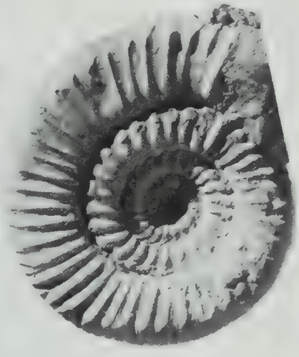
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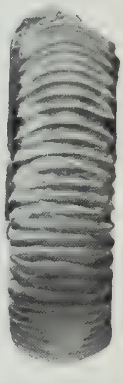
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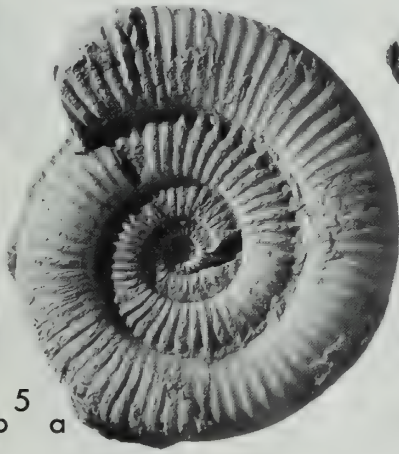
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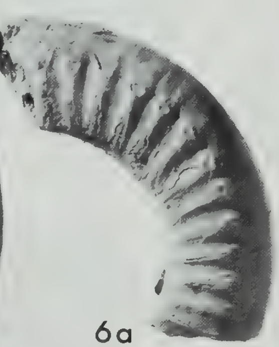
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to be nearly complete and would have had its adult mouth border before reaching 30 mm diameter. One of the fragments has septa up to 16 mm diameter, and in all the others septation ceases at smaller sizes. A rather smaller, but complete, adult is figured in Pl. 9, fig. 4. This is 22·2 mm in diameter at the mouth border, has $\frac{13}{16}$ whorl of body chamber, and final approximated suture-lines at 14 mm diameter; it also shows that the keeled venter becomes progressively rounded on the last half whorl of the adult body chamber. Two more specimens (Pl. 9, figs 6, 7) are nearly adult, but neither is quite complete; they both have $\frac{3}{4}$ whorl of body chamber and the blunt keel on the venter is beginning to be lost just before the aperture.

The angled or keeled venter on all whorls except the final half whorl of the adult body chamber is accentuated by the raised sharp secondary ribs in the middle of the venter. It is a unique feature of this species that is not found in whorls of *Z. braunianus* of the same size, where the ribs may sometimes be raised and sharp in the middle of the venter, but no prominently keeled venter is formed. The ribs are variable in strength and density; they are often fairly strong and widely spaced at 7–15 mm diameter, then become smaller and dense on the last half whorl of the body chamber. Small, sharp ventrolateral tubercles are usually formed on the final whorl, but they may be feeble or absent on the earlier whorls with ventral keels.

The type specimens of *Z. pseudobraunianus* were described by Monestier (1931 : 54) from the Bifrons Zone at Aveyron. The lectotype is the largest of them and has a maximum size of 21 mm diameter; it is similar in shape and ornament to the Northampton specimen of Pl. 9, fig. 7. Another Aveyron specimen was made the type of the new genus and species *Gabillytes larbusselensis* by Guex (1971 : 239). It does not differ from *Z. pseudobraunianus* in having stronger ribs, as claimed by Guex, because it is only 10·7 mm diameter (Guex's figure (1971 : pl. 2, fig. 2) is enlarged to approximately × 2·4); in fact it agrees very closely in rib strength and density with the lectotype of *Z. pseudobraunianus* at the same size. It also agrees closely with the penultimate whorls of several of the Northampton specimens. Guex's specimen appears to be a juvenile, and not an adult as he claims, because its strongly ribbed and keeled final half whorl is characteristic of the penultimate whorl of the Northampton specimens, which become adult at 22–30 mm diameter after further growth of about one whorl on which the ribs become more dense and the keel is progressively lost. The notion also put forward by Guex (1971 : 235) that this species and the genus *Gabillytes* are microconchs, for which the corresponding macroconchs are represented by *Z. braunianus*, is not thought to be correct. *Z. pseudobraunianus* has a keeled venter that is mainly characteristic of the last septate whorl. Such a keel is not found in *Z. braunianus*, and it seems difficult to substantiate a claim that a pair of forms are dimorphic, when there are morphological differences at similar growth stages that do not include the adult body chambers of either form.

Genus ***PORPOCERAS*** Buckman 1911

TYPE SPECIES. *Ammonites vortex* Simpson 1855.

SYNONYM. *Telodactylites* Pinna & Levi-Setti 1971 (type species: *Ammonites desplacei* d'Orbigny 1844).

Plate 9 **× 1 (Figs 4–7, × 1·5)**

Porpoceras verticosum Buckman, Fibulatum Subzone

Fig. 1. 1–2 m below top of Bifrons Zone Clays below Northampton Sand ironstone, ironstone quarry (SK 878309), Harlaxton, 6 km south-west of Grantham, Lincolnshire; BM C.69564.

Porpoceras vortex (Simpson), Fibulatum Subzone

Fig. 2. Same horizon and locality as Fig. 1; BM C.69565.

Fig. 3. Upper *Leda ovum* Beds, Corby, Northamptonshire; Northampton Museum, B. Thompson Colln.

Zugodactylites pseudobraunianus (Monestier), Fibulatum Subzone

Figs 4–7. Lower *Leda ovum* Beds, Vigo brickpit, Northampton; all × 1·5. Fig. 4, BM C.79465. Fig. 5, BM C.67531. Fig. 6, BM C.79463. Fig. 7, BM C.79464.

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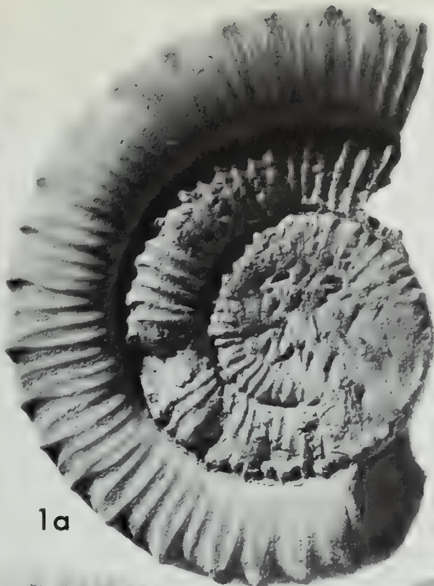
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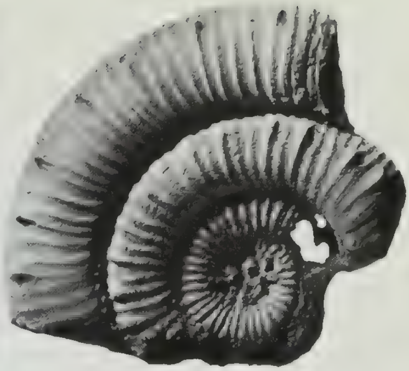
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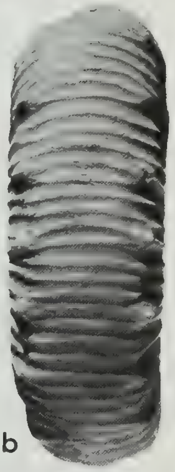
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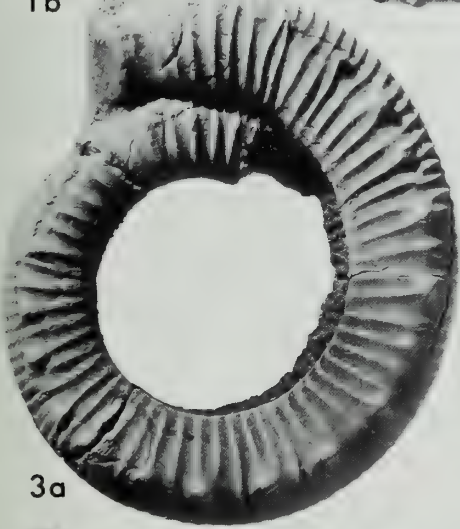
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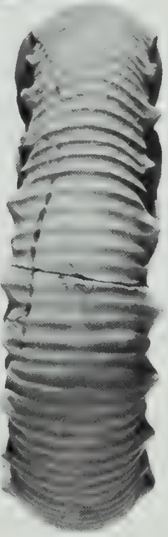
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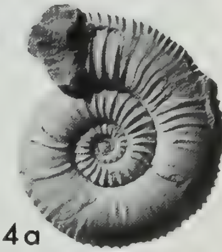
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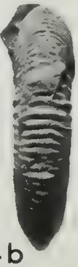
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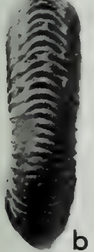
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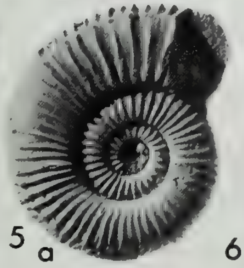
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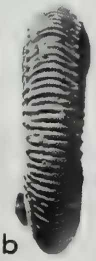
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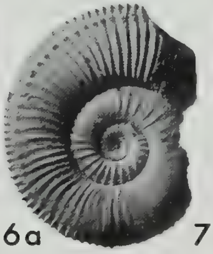
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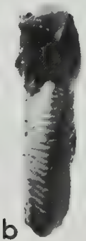
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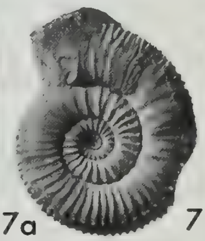
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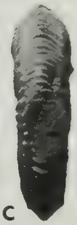
7c

Diagnosis. Whorl section varies between square and depressed. Ventrolateral tubercles occur on every second, third or fourth rib. The primary ribs on the side of the whorl are sometimes looped in pairs to tubercles, but this character is not constant as in *Peronoceras*. One to three non-tuberculate ribs occur between each tuberculate rib. Ribs on the venter are continuations of the non-tuberculate primary ribs, or issue in pairs from the ventrolateral tubercles, or a few are intercalated.

Distribution. Fibulatum Subzone, upper part. Northamptonshire: Upper *Leda ovum* Beds. Yorkshire: Whitby bed 72 (lower 1·5 m), Ravenscar beds xlii and xliii.

Remarks. Three British species are known, *P. vortex* (Simpson), *P. verticosum* Buckman (1914 : pl. 91) and *P. vorticellum* (Simpson) (Buckman 1913 : pl. 90), which occur at a single horizon in Yorkshire, Lincolnshire and Northamptonshire. This is near the top of the Fibulatum Subzone, well above the range of *Peronoceras* and *Zugodactylites*, and below the lowest *Catacoeloceras* at the base of the Crassum Subzone. The three species are commonest at Ravenscar, Yorkshire, in beds xlii and xliii (Howarth 1962*b* : 400). From a study of the considerable numbers of specimens present it seems that the three species are closely related, all having the special fibulation and tuberculation characters of *Porpoceras* as distinct from *Peronoceras*. They differ from each other mainly in the much-depressed whorls of *P. vortex*, the less depressed, almost square whorl section of *P. verticosum*, and the closely similar whorls, but denser, weaker ribs and weaker tubercles, of *P. vorticellum*. If a much larger collection were available with more complete adults it might be possible to suggest that all three were variants of a single species. Pinna & Levi-Setti's (1971 : 107, 121) separation of *P. verticosum* and *P. vorticellum* from *P. vortex*, by referring the two former to *Nodicoeloceras*, is not correct. Species of *Peronoceras* with square or depressed whorls, such as *P. subarmatum* and *P. perarmatum*, are distinguished by having much more consistent fibulation on at least their inner whorls, where the ventrolateral tubercles are larger and developed as spines when the shell is complete. The alternating nature of the tubercles and single ribs in *Porpoceras* and the varying amount of fibulation make the genus distinctive.

In addition to the two Northamptonshire examples of *P. vortex* from the Upper *Leda ovum* Beds that are described below, several specimens are known from the Grantham area. *P. vortex* and *P. verticosum* were collected by Trueman (1918 : 107) from his bed 8, about 6 m below the top of the Lias, immediately south of Grantham. Three *P. vortex* and one *P. verticosum* were collected many years ago by the Institute of Geological Sciences at Grantham (GSM 22515–18). More recently two fine specimens (Pl. 9, figs 1, 2) have been found 1–2 m below the top of the Lias in ironstone quarries at Harlaxton (SK 878309), 6 km SW of Grantham.

Porpoceras vortex (Simpson 1855)

Pl. 9, figs 2, 3

1855	*Ammonites vortex* Simpson : 60.
1905	*Coeloceras* (*Peronoceras*) *desplacei* (d'Orbigny); Joly : 10; pl. 2, figs 1–5.
1911	*Porpoceras vortex* (Simpson) Buckman : pls 29A, 29B.
? 1966	*Peronoceras vortex* (Simpson) Pinna : 118; pl. 6, figs 16, 18.
? 1966	*Peronoceras vortex* (Simpson); Fischer : 42; pl. 2, fig. 5.
1971	*Peronoceras vortex* (Simpson); Pinna & Levi-Setti : 121; pl. 11, fig. 7; pl. 12, fig. 9.
1972	*Porpoceras vortex* (Simpson); Guex : pl. 8, fig. 16.

Holotype. Whitby Museum no. 153a, figured by Buckman (1911 : pl. 29A).

Description. There are two examples of this species from the Upper *Leda ovum* Beds at Corby in Beeby Thompson's collection. The better-preserved specimen (Pl. 9, fig. 3) consists of slightly more than one whorl which is a complete adult body chamber with a marked constriction at the mouth border at 76 mm diameter. Almost all the whorl is crushed laterally so that the whorl breadth appears to be too small for this species, but there is a short length of uncrushed whorl just after the final suture-line, which has a whorl height of 13·0 mm and a whorl breadth of 21·0 mm at about 45 mm diameter. Comparing these dimensions with those of the type specimens of the three Yorkshire species (Buckman 1914 : 91*b*), it is clear that the specimen can only belong to

P. vortex. The second Corby specimen consists of half a whorl of about 70 mm maximum diameter and is not well preserved. Both specimens have a ventrolateral tubercle on approximately every third rib and some of the primary ribs are looped in pairs to the tubercles.

A specimen from an ironstone quarry at Harlaxton, Lincolnshire, is figured for comparison (Pl. 9, fig. 2). It has final suture-lines at about 47 mm diameter, and the aperture after nearly a whorl more is close to the adult mouth border at about 70 mm diameter. *P. verticosum*, which also occurs at Harlaxton (Pl. 9, fig. 1) and other localities near Grantham, differs in its square whorl section. *P. vortex* is common in beds xlii and xliii at Ravenscar, Yorkshire, where complete adults range between 70 and 110 mm maximum diameter.

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A. W. Gentry & A. Gentry

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Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part I

Alan William Gentry and **Anthea Gentry**

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Synopsis

A revision of the fossil bovids from Olduvai Gorge, Tanzania, is given, and they are compared with those of other published sites in East and South Africa. The new species *Syncerus acoelotus* and *Damaliscus agelaius* are described. A neotype is erected for *Megalotragus kattwinkeli* (Schwarz). In the second part of the work is an account of the bovids from each site at Olduvai. This paper covers all material brought out of the Gorge until January 1971 and some later material.

Introduction

Olduvai Gorge, formerly called Oldoway or Duwai Gorge, is famous as one of the foremost sites in the world for the remains of early man. It lies in a corner of the Serengeti Plains of northern Tanzania at 2°59′ S 35°21′ E, a little to the west of the eastern Rift Valley. The gorge runs eastwards from Lake Elgarja or Lgarya (also called Lake Ndutu) and cuts into Pleistocene beds. After about 37 km it joins up with a side gorge from the south and after another 9 km drains into the Balbal depression at the foot of the Ngorongoro–Olmoti highlands. The earliest European traveller in this part of Tanzania was Dr Oscar Baumann in March 1892 who used the name Duvai for the small hill about 15 km south-east of Lake Elgarja, but the discovery of mammalian fossils in the nearby gorge was left to Professor Kattwinkel of Munich, or perhaps Mrs Kattwinkel (Branca 1914 : 1171), in or shortly before 1911. The fossiliferous beds were explored more thoroughly in October to December 1913 by a German expedition under the leadership of Professor Hans Reck. Further expeditions were abandoned because of the outbreak of the First World War, but a series of faunal reports was initiated (Dietrich 1916, and from 1925 onwards the articles in the series entitled *Wissenschaftliche Ergebnisse der Oldoway-Expedition 1913*). The 1913 expedition found no artifacts, but had excavated a human skeleton which became the subject of a long controversy before being accepted in 1935 as an intrusive burial of *Homo sapiens*. M. D. Leakey (1971b : 225) gives a summary and further references on this important aspect of the early studies at Olduvai Gorge. Notwithstanding the ultimate verdict on the skeleton, it helped to maintain interest in the Gorge. In the late 1920s Dr L. S. B. Leakey became concerned about how to correlate his own human and faunal finds in Kenya with those at Olduvai. The human fossils were similar but the accompanying fauna was much younger than at Olduvai.

Accordingly he twice visited Professor Reck in Berlin, and eventually Reck joined his East African Archaeological Expedition of 1931–32 which worked at Olduvai. The expedition relocated the site where the human skeleton had been found 18 years earlier. Of greater interest for us today was the recovery of more fauna and the discovery that artifacts were present in all levels. Leakey did much more work at Olduvai in later years and tried to establish a sequence of stages for the evolution of the stone tool cultures. His results were presented in Leakey (1951). For a long time fossils of hominids remained scarce. Two cranial vault fragments were discovered in 1935, a hominid molar tooth and canine in 1955, and another hominid molar tooth in June 1959. Then on 17 July 1959 came the discovery by M. D. Leakey of one of the most famous skulls in African prehistory, that of the australopithecine which was later named *Zinjanthropus boisei* (Leakey 1959). Thereafter the Leakeys obtained financial support for more intensive excavations of hominid occupation sites.

It has now become clear that the Olduvai deposits span a period going back to the start of the Pleistocene. Reck (1914 : 84; *in* Leakey 1951 : 5) outlined the stratigraphy, and proposed a division into five beds numbered I, II, III, IV and V from below upwards. The first four of these beds have been found satisfactory in the subsequent geological work of R. L. Hay (1963, 1967, 1971, 1976), although he points out that in modern stratigraphical practice the beds would be considered formations. According to Hay, seven beds are present above basement rocks and together they reach a maximum exposed thickness of 100 m. The beds were laid down in a shallow basin under arid or semi-arid conditions. Bed I, of exposed thickness varying from 18 to 43 m, and the lower part of Bed II were laid down unaccompanied by much faulting and comprise the lower sequence. Many of the constituent rocks of Bed I are volcanic trachytes, clays and lava flows, and palaeosols are frequent. A shallow, saline lake occupied part of the western area of the sequence and there were lake margin and alluvial fan deposits to its east. Nearly all Bed I fossils come from east of the lake.

The onset of widespread faulting gave rise to a major depositional disconformity. Thereafter the middle and upper parts of Bed II above the Lemuta Member, itself underlying the disconformity, and Beds III and IV were laid down in an alluvial plain with a much smaller lake. There are mainly clays, sandstones and conglomerates from the start of middle Bed II upwards. The entire Bed II is 20–30 m thick, and Beds III and IV up to 45 m. Beds III and IV are distinguishable as two separate units only in the eastern part of the Gorge. On top of Bed IV are the Masek Beds, the deposition of which ceased when the subsidence of Balbal lowered the base level sufficiently to cause erosion of the Gorge.

The Ndutu Beds, constituting the older part of the former Bed V, were deposited after the Gorge had attained about three-quarters of its present depth. Following the latest known faulting in the region, these beds were themselves eroded and the Gorge cut to its present depth. The Naisiusiu Beds were laid down during the period from a little over 20 000 to 15 000 years ago.

Potassium-argon (K-Ar) studies have given a date of 1·79 million years for Tuff IB (Evernden & Curtis 1965 : 354; Curtis & Hay 1972 : 295). The same tuff gave an age of 2·03 ± 0·28 million years by the entirely independent method of fission-track dating (Fleischer, Price, Walker & Leakey 1965 : 72). Considerable overlap of K-Ar dates for the Bed I tuffs suggests a probable deposition period of as little as 130 000 years for the greater part of Bed I (Curtis & Hay 1972 : 293–294). The mean age for Bed I is 1·82 ± 0·13 million years. Dates from higher levels are more uncertain, but palaeomagnetic and other studies have been combined to produce the suggestions of 1·7 million years for the top of Bed I, 1·15 million years for the top of Bed II, 0·8 million years for the top of Bed III and 0·6 million years for the top of Bed IV (Hay 1976). Beds I to IV would thus be encompassed in that part of the Pleistocene which ended with the onset of the Mindel or Elsterian glaciation in continental Europe (Berggren & van Couvering 1974 : 92, fig. 11). They would be largely of Lower Pleistocene age.

The family Bovidae is one of the most abundant mammal groups at Olduvai. M. D. Leakey (1971b : 257, table 4) shows the numbers of bones of larger reptiles and mammals occurring at the excavated sites. In this grouping, which excludes rodents, bats and insectivores, the percentages of bovids go as high as 80·9. We calculated the mean value for the 21 bovid entries in this table as 51·8 %. Studies of the Olduvai bovids have been made previously by Reck (1928, 1935, 1937) and

Schwarz (1932, 1937), who described material in Berlin and Munich which had been collected by the expedition of 1913. This material came entirely from Beds II, III and IV; none was from Bed I. Hopwood (1934, 1936) and Leakey (1951) worked on material in London collected by the Third and Fourth East African Archaeological Expeditions of 1931–32 and 1934–35. Leakey (1965) made new identifications of some of the earlier material, and also began the descriptions of material from the new excavations. Gentry (1965, 1966, 1967) revised some of the tribal and generic assignments. Cooke (1963) compared the East African fossils with those from South African sites.

There are collections or examples of Olduvai antelopes in the Institut für Paläontologie und Museum der Math.-Naturwissenschaftlichen Fakultät der Humboldt-Universität, Berlin (the type specimen of *Pelorovis oldowayensis*), the British Museum (Natural History), London (material from the years 1931–35 inclusive), the National Museum of Kenya, Nairobi (material recovered after 1935) and the National Museum of Tanzania, Dar es Salaam. Nearly all the material formerly in the Paläontologischen Staatssammlung in Munich, which included Schwarz's (1932, 1937) type specimens, was destroyed during the Second World War. The only exceptions are the single cranium of *Thaleroceros radiciformis* and a few primates. We visited Munich in July 1969 and were assured by Professor Dr R. Dehm and Dr F. Obergfell that all the Olduvai material that survived the war has now been unpacked, and that none remains in storage. Thus nearly all of the material collected by the expedition of 1913 has been lost.

In this work we have revised the identification and classification of many Olduvai bovids, referred for the first time to much of the material excavated in the 1960s and compared the bovid fauna with that of other East African and some South African sites (see Fig. 37 in Part II of this paper). We have also made comparisons with published north African material.

Omo in southern Ethiopia, particularly the Shungura Formation, is an important comparative site. Arambourg collected there in 1932–33, and there has been a series of French and American expeditions since 1967 (see Arambourg 1941, 1947; Howell 1968; Coppens 1973). The succession consists of a basal member followed in ascending order by members A to L. Radiometric dates given by Brown (1972) include 2·16–2·56 million years for Tuff D at the base of member D and 1·81–1·87 million years for Tuff I_2 in member H. Recent palaeomagnetic work by Brown and others suggests that the formation spans the age range 3·2 to 0·9 million years and that member H correlates in time with Olduvai Bed I. Both the French and American parties and a Kenya expedition of 1967 have collected fossils from the Usno and the Mursi Formations at Omo, the former having a K-Ar date of nearly 3 million years and the latter about 4 million years.

Fossils from the Pliocene–Pleistocene beds at Kaiso, Uganda, have been revised by Cooke & Coryndon (1970) and include some bovids. They point to the existence of two faunal levels, and material from Nyabrogo and Nyawiega is thought to be earlier than that from Kaiso Village and Behanga.

In the 1930s Leakey's expeditions collected fossils from a number of localities on the southern shore of the Kavirondo Gulf, Lake Victoria. Kent (1942) mentioned Kanam East, Kanam West, Kanam Central and Kokkoth in the oldest Kanam Beds; Rawe, Fish Cliff, Kagua and probably Kanam East Hot Springs in the next oldest Rawe Beds; and Kanjera in the younger Kanjera Beds.

Expeditions to Peninj near Lake Natron, Tanzania, were organized in 1963 and 1964. The fossils, which are now in Dar es Salaam, nearly all came from the Humbu Formation which is probably contemporary with the upper part of Olduvai Bed II above the Lemuta Member (Isaac 1967 : 251). Isaac & Curtis (1974) suggest an age of the order of 1·0–1·5 million years, on the basis of palaeomagnetic data and K-Ar dating. In relation to the individual fossils mentioned in the present paper, the initials BSC refer to basal sandy clays below the Limestone and Basaltic Tuff Member, MZ to the sediments immediately above this member and USC to the upper sandy clays from there to the base of the overlying Moinik Formation.

The Laetolil area (Kent 1941; M. D. Leakey *et al.* 1976) is about 20 miles south of Olduvai close to the north-western shore of Lake Eyasi. Fossil mammals were collected from the surface of terrestrial deposits there by Kohl-Larsen in 1938–39, and by Leakey in 1935, 1959 and 1964. Kohl-Larsen's material is now in Berlin, Leakey's 1935 material in London and his 1959 and 1964 material in Nairobi. Kohl-Larsen had also collected in 1935–36 from nearby later deposits at the north end of Lake Eyasi (=Njarasa See). Dietrich (1942 : 50) wrote that the 'old fauna' of Kohl-Larsen was found in the valleys of the Vogel River, Deturi, Oldogom, Garussi, Gadjingero and Marambu. The first site of this list is Laetolil in the restricted sense and is apparently the site originally worked by Leakey (Maglio 1973 : 69). However, the 'old fauna' at all the sites is derived from the Laetolil Beds (=the Vogel River Series of Maglio 1973 : 72, *ex* Bishop). Later deposits are present in the Laetolil area, and some mixing takes place of the fossils of the old fauna with younger fossils. Maglio (1970 : 331; 1973 : 69–72) recognized at least two discrete faunal levels in the Laetolil material, one coming from the Laetolil Beds and the other dating from just before Bed I. Most bovids from the Laetolil area are unlike Olduvai species, and clearly belong to the 'old fauna' of the Laetolil Beds. M. D. Leakey *et al.* (1976) have given K-Ar dates for this fauna of between 3·59 and 3·77 million years. However, a few of the fossils collected by Leakey in 1959 are much more recent and must be coeval with or later than Olduvai. The specimens include horn cores of *Connochaetes taurinus* and a subfossil horn core of a Grant's gazelle.

We visited museums in South Africa in 1969 and 1971. In the South African Museum, Cape Town, we saw bovids from the Cape Province sites Langebaanweg, Elandsfontein (=Hopefield), Melkbos and Swartklip. In the National Museum, Bloemfontein, we saw material from Cornelia, Florisbad, Vlakkraal (=Prinsloo), Mahemspan and other Orange Free State sites, and in the Bernard Price Institute for Palaeontological Research, Johannesburg, we saw material from Makapansgat Limeworks in the Transvaal. The bovid faunas at several of these sites were reviewed by Wells (1967). The geology and fauna, including antelopes, of Melkbos and Langebaanweg were discussed in three papers by Hendey (1968, 1970a, 1970b) and of Swartklip by Hendey & Hendey (1968). The bovids from Makapansgat Limeworks have been studied by Wells & Cooke (1956) and those of Cornelia by Cooke (1974). A preliminary survey of the Langebaanweg bovids was made by Gentry (*in* Hendey 1970a), but several identifications are now known to have been incorrect. Wells (1969a) and Hendey (1969) have considered the probable age of these and other South African sites, and Hendey (1974 : 56) has based a sequence of mammal ages on them. Hendey's post-Miocene sequence and placing of the above-mentioned sites is:

Langebaanian	Langebaanweg
Makapanian	Makapansgat Limeworks
Cornelian	Cornelia, Elandsfontein
Florisian	Florisbad, Vlakkraal, Mahemspan, Melkbos, Swartklip.

Some Elandsfontein material is thought to be of Florisian age, and some Langebaanweg (Baard's Quarry) of Makapanian age. Apart from one or two specimens we did not see material from the Vaal River Gravels described by Cooke (1949), or from the following Florisian sites: Cave of Hearths and Kalkbank (Cooke *in* Mason 1962), and Wonderwerk Cave (Cooke 1941; Wells 1943).

Little radiometric dating is possible for these sites. The Peat Layer I at Florisbad, from which the fauna came, has ^{14}C dates ranging from above 35 000 to above 48 000 BP, and the Middle Stone Age levels of the Cave of Hearths from below 18 000 BP (Deacon 1966 : 27, 28). However, a new series of dates from South Africa and other lines of evidence suggest that the entire Middle Stone Age spanned a period from upwards of 100 000 until 40–30 000 BP (Beaumont 1973 : 46; Klein 1974b : 257). Consequently both Cave of Hearths and Florisbad are likely to be very much older than originally thought.

We have seen material in the British Museum (Natural History) from the middle Pleistocene site of Broken Hill, now Kabwe, Zambia (Clark 1959), and from the middle Pleistocene of the Chiwondo Beds, Malawi, reported on by Coryndon (1966).

Anatomical measurements in this paper are given in millimetres. However, geological measurements, quoted from the most recent workers at Olduvai, are given in imperial units, and we have added the metric equivalents for convenience.

Horn cores are described as obliquely inserted when their inclinations are low in side view. This is the opposite condition from having upright insertions.

We have used the designation 'upper molar' in relation to isolated teeth without trying to differentiate M^1, M^2 and M^3. However with isolated lower teeth we have specified M_3 separately, so that 'lower molar' includes only M_1 and M_2.

A basal pillar is a pillar in the centre of the medial edge of the upper molars or the lateral edge of lower molars, completely or partly separate from the rest of the occlusal surface. The upper basal pillar is the entostyle and the lower the ectostylid.

A goat fold is a transverse flange at the front of the lower molars of some bovid groups.

Measurements of length on limb bones were taken as follows:

Femur from the lateral end of the articular head to the lowest level of the distal medial condyle.
Tibia from the lowest point of the top medial facet to the projecting tip behind the medial malleolus.
Metatarsal from the highest point behind the medial part of the ectocuneiform facet to the medial side of the most projecting part of the distal medial condyle.

STRATIGRAPHY		SITES	
Naisiusiu Beds			
Ndutu Beds			
Masek Beds		FLK	
Aeolian tuff			
BED IV		GC GTC WK group PDK HEB group LK and RK	BK Bos K Hoopoe Gully VFK
		EF-HR	
BED III		JK2 GP8 JK1 JK2 JK group	
BED II upper	IID	BK FK West Kar K Rhino K TK	GRC MRC
	IIC	Kit K	
middle	IIB	SHK EF-HR Elephant K MNK Occupation Site FC West	Long K FLK
		MNK Skull Site HWK East levels 3-5 Sandy Conglomerate HWK EE	
IIA Lemuta Member			
lower	IF	FLKN Clay with root casts HWK East levels 1-2 HWK FLK West	
			?FLKN Ostrich Site
BED I	ID	HWK FLKN levels 1-6	VEK KK MJTK
	IB	FLK FLKNN	
		DK THC	
Basalts of Bed I			

Fig. 1 Sites where bovids have been found at Olduvai Gorge since the Second World War, shown in relation to the stratigraphy. Some of the tuffs from IB to IID are also shown.

Humerus from the top of the lateral tuberosity to the lowest point of the medial side distally.

Radius from the centre of the medial edge of the proximal medial facet to the lowest point of the ridge on the medial side of the scaphoid facet.

Metacarpal from the edge of the proximal articular facet above the insertion for the extensor carpi radialis to the median side of the most projecting part of the distal medial condyle.

Fossils at Olduvai have been found on the surface or have been excavated from sites named according to a convention using groups of initials, e.g. BK or SHK (see M. D. Leakey *in* L. S. B. Leakey 1965 appendix 2; M. D. Leakey 1971b). Fig. 1 shows the position of many of these sites in relation to the stratigraphy of the Gorge. In this paper a specimen designation such as BK II 1953.85 means site BK in Bed II during the year 1953, specimen number 85. BK II 1963.067/1648 indicates an unnumbered specimen found in 1963 in BK II which in 1967 was given the number 1648. 068 is the prefix for similar specimens numbered in 1968. Sometimes the subdivisions of Bed II are given, e.g. FC West middle Bed II 1963.201. Material gathered from Olduvai in 1941 was given numbers prefixed by 'F', as in F.3001. In recent years single fossil finds have been given numbers prefixed by 'S', e.g. S.38, in which the initial stands for 'sundry'. The abbreviations P.P.F., P.P.R. and P.P.T. refer to short lists of figured, referred and type material in Nairobi. BM(NH) is the abbreviation for the British Museum (Natural History), KNM for the National Museum of Kenya, Nairobi, SAM for the South African Museum, Cape Town, and BPI for the Bernard Price Institute for Palaeontological Research in Johannesburg. Text references to works by L. S. B. Leakey are given as 'Leakey', and other members of his family are distinguished by their initials. Photographs of some of the best Olduvai fossils mentioned in this paper are given in Leakey (1965).

Acknowledgements

We thank Dr M. D. Leakey and the late Dr L. S. B. Leakey whose many years of work at Olduvai Gorge have made available the antelope collections which we describe. Professor H. B. S. Cooke allowed us to see unpublished papers, and Mr J. W. Simons provided information about Olduvai bovines. Professor R. L. Hay identified some matrix samples and discussed geological matters. Dr M. D. Leakey kindly read an earlier draft of this paper with great care. Professors Hay and Cooke also made helpful comments on the text. Mr R. I. M. Campbell photographed nearly all the Nairobi specimens which we wished to illustrate, and Mr J. Leonard took photographs of a few others. Dr J. van Heerden photographed the *Damaliscus niro* frontlet in Bloemfontein. We are grateful for the assistance of the staffs of the museums and institutes in Nairobi, Dar es Salaam, Cape Town, Bloemfontein, Johannesburg, Pretoria, London, Munich and Berlin.

Much of the cost of our travels in connection with this work was borne by the Wenner–Gren Foundation for Anthropological Research in New York.

Systematics

In this paper the following classification of bovids will be followed:

Family BOVIDAE	
Subfamily BOVINAE	
Tribe TRAGELAPHINI	kudus, bushbuck and related antelopes.
Tribe BOSELAPHINI	now represented by only two tragelaphine-like antelopes in India, but formerly occurring in Africa. None found at Olduvai Gorge.
Tribe BOVINI	cattle and buffaloes.
Subfamily CEPHALOPHINAE	
Tribe CEPHALOPHINI	duikers, small forest antelopes only rarely fossilized and not found at Olduvai Gorge.

Subfamily HIPPOTRAGINAE	
Tribe REDUNCINI	reedbucks, kob, lechwes and waterbuck.
Tribe HIPPOTRAGINI	roan, sable, oryxes and addax.
Subfamily ALCELAPHINAE	
Tribe ALCELAPHINI	wildebeest and hartebeest group, impala.
Subfamily ANTILOPINAE	
Tribe NEOTRAGINI	dik dik and other small antelopes.
Tribe ANTILOPINI [incl. Saigini]	gazelles, springbok.
Subfamily CAPRINAE	
Tribe 'RUPICAPRINI'	goral and serow group, not found in Africa. (*Rupicapra* itself might be better placed in the Caprini.)
Tribe OVIBOVINI	muskox, takin and extinct allied forms.
Tribe CAPRINI	sheep and goats.

More detailed information will be found under the tribal headings.

Tragelaphines are rare at Olduvai except for two temporal subspecies of the greater kudu. Two lineages of Bovini, two of Reduncini and an extinct *Hippotragus* are moderately common. The Alcelaphini and an extinct springbok are well represented at the Gorge. A number of other forms occur as rarities.

Tribe **TRAGELAPHINI**

Living members of the tribe are the sitatunga, bushbuck, greater and lesser kudus, nyala, mountain nyala and bongo which are all placed in the genus *Tragelaphus*, and the eland placed in *Taurotragus*. They are medium to large antelopes with spiralled horns and rather brachyodont teeth, which live where there is cover or even forest and feed mainly by selective browsing. Their characteristic skull features are: horn cores keeled, spiralled (torsion anticlockwise from the base upwards on the right side), inserted obliquely and behind the orbits. Frontals between the horn core bases slightly raised above the level of the top of the orbital rims, braincase little angled on the facial axis and sometimes widening posteriorly in dorsal view, side wall of the braincase with a depression below and behind each horn core base, no postcornual fossae, the front of the orbit tending to lack a rim along the lachrymal edge, nasals long and narrow, ethmoidal fissures large, no preorbital fossae, infraorbital foramen low over the tooth row and anteriorly placed, premaxillae rising as far as the nasals in side view and narrowing anteriorly to a blunt end in ventral view, occipital surface tending to be flattened, mastoids small, basioccipital long with a central transverse constriction and anterior tuberosities passing in front of the level of the foramina ovalia. Teeth rather brachyodont, basal pillars small or absent on lower molars and absent on upper molars, central cavities without a complicated outline, upper molars without prominently outbowed ribs between the styles, lower molars with narrowly pointed lateral lobes and without goat folds, premolar rows long and P2s large, P_4s often with paraconid–metaconid fusion which closes the anterior part of the medial wall, and mandibles with shallow horizontal rami.

Tragelaphus scriptus (Pallas 1766), the bushbuck, was once common in most of Africa south of the Sahara, living mainly in bush or lightly wooded country. It is small to medium-sized and has anteroposteriorly compressed horn cores with the posterolateral keel the main one.

Tragelaphus spekei P. L. Sclater 1864, the sitatunga, lives in swamps in parts of Africa as far south as the extreme north-east of Namibia (South West Africa). It is medium-sized and has long hoofs and longer horns than in the smaller bushbuck.

Tragelaphus angasi Gray 1849, the nyala, is medium-sized and found in woodlands with thickets in restricted parts of south-east Africa. The males have manes along the top of the back and on the centre of belly and neck.

Tragelaphus imberbis (Blyth 1869), the lesser kudu, usually occurs in rather dense thickets in bush-covered desert in parts of east Africa from Somalia southwards. It may also occur in Arabia (Harrison 1972 : 629). It is medium-sized and has horn cores differing rather indistinctly from those of the sitatunga by being longer, more spiralled, less divergent, and with a less strong posterolateral keel.

Tragelaphus strepsiceros (Pallas 1766), the greater kudu, is absent from north and west Africa. It is a large antelope and has large and strongly spiralled horn cores with an anterior keel and no anteroposterior compression. It lives in hilly country and thickets, even in fairly arid country.

Tragelaphus buxtoni (Lydekker 1910), the mountain nyala, is endemic to the Ethiopian highlands east of the Rift Valley, living in forests, heath and grasslands around 3000–3500 m. It is medium-sized to large and in some features of its horn cores resembles the greater kudu.

Tragelaphus eurycerus (Ogilby 1837), the bongo, is discontinuously distributed in thick forest of west Africa, Zaïre (Congo) and east Africa. It is large and short-legged and both sexes have horns.

Taurotragus oryx (Pallas 1766), the eland, is the largest tragelaphine and occurs in much of Africa south of the Sahara. It has horn cores in both sexes with a strong anterior keel, without anteroposterior compression, quite tightly twisted about their axes but less openly spiralled than in any other tragelaphine. It avoids dense cover but otherwise is found in a wide range of habitats like the greater kudu.

Genus *TRAGELAPHUS* Blainville 1816

TYPE SPECIES. *Tragelaphus scriptus* (Pallas 1766).

GENERIC DIAGNOSIS. Medium to large tragelaphines with spiralled horn cores inserted close together and having an anterior keel and sometimes a strong posterolateral one; small to medium-sized supraorbital pits, which are frequently long and narrow; occipital surface tending to have a flat top edge and straight sides.

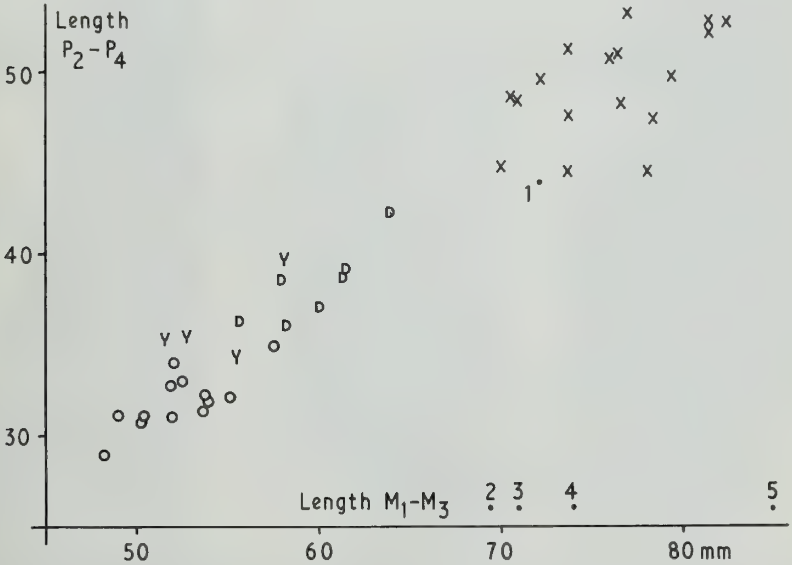


Fig. 2 Length of lower premolar row plotted against length of lower molar row for some tragelaphines.

X = Recent *Tragelaphus strepsiceros*, D = *T. imberbis*, Y = *T. angasi*, O = *T. spekei*, 1 = *T. strepsiceros maryanus* FLK I 067/1100.

Molar row lengths are also shown for the following: 2 = FLKN I 882, 3 = FLKNN I 66+548, 4 = DK I 3001, 5 = Peninj A67.270+A67.277. 2, 3 and 4 are *T. s. maryanus*, while 5 is probably *T. s. grandis*.

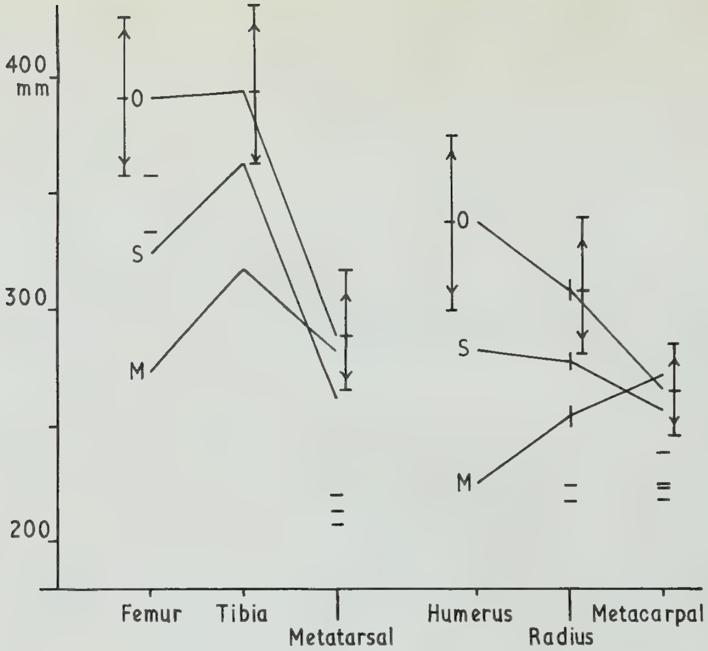


Fig. 3 Lengths of limb bones in Tragelaphini.

O = mean of 9 *Taurotragus oryx*, with vertical lines showing ranges and standard deviations. S = mean of 3 Recent *Tragelaphus strepsiceros*. M = mean of 3 *T. imberbis*.

Horizontal dashes indicate Tragelaphini from Olduvai, all from Bed I except the larger of the femora, which is from BK II. The BK II femur is probably *Tragelaphus strepsiceros grandis*, the Bed I femur has not been identified and the other limb bones are smaller than would be expected for *T. s. maryanus*.

Tragelaphus strepsiceros (Pallas 1766)

Diagnosis. A large species of *Tragelaphus* with strongly and openly spiralled horn cores, anterior keel present but posterolateral keel reduced and tending to be present only distally; compared with other *Tragelaphus* species the horn cores are more uprightly inserted and are not anteroposteriorly compressed; braincase short; a low occipital.

Tragelaphus strepsiceros maryanus (L. S. B. Leakey 1965)

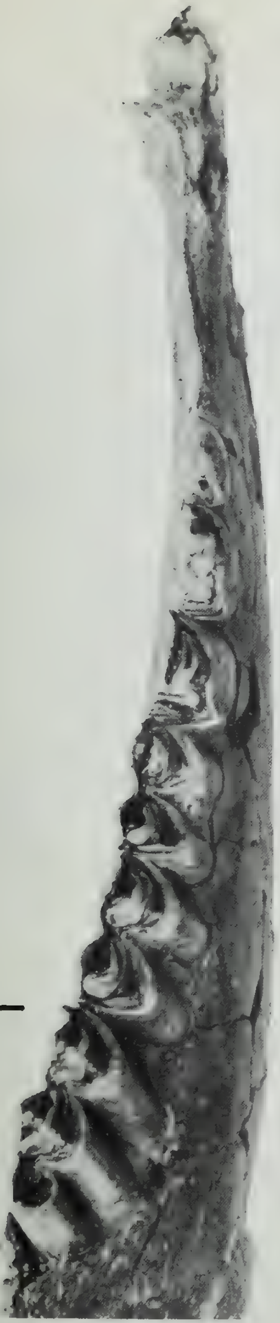
1965 *Strepsiceros maryanus* Leakey : 40, pls 40–42.

Diagnosis. A subspecies of *Tragelaphus strepsiceros* differing from the living greater kudu in having horn cores with more mediolateral compression, the braincase top more angled on the facial axis, and fusion of paraconid with metaconid on all known P_4s.

Holotype. A cranium with almost complete horn cores found in 1959 and now in Dar es Salaam.

Horizon. The holotype came from level 2 of HWK East, lower Bed II, Olduvai (Leakey 1965 : 41; M. D. Leakey, personal communication) although it is inscribed ‘Olduvai 1959 EKK *Strepsiceros maryanus* TYPE’. Other specimens are moderately common in Bed I, lower Bed II and perhaps early in middle Bed II.

Remarks. A frontlet of *Tragelaphus strepsiceros maryanus* with nearly complete horn cores, dentitions and partial skeleton came from FLKNN I in 1960, and a cranium 068/5813 from KK II in 1959. (Leakey states (1965 : 42) that both specimens came from Bed I.) The latter has a very strongly inclined top of its braincase. Dentitions assigned to *T. s. maryanus* are slightly smaller



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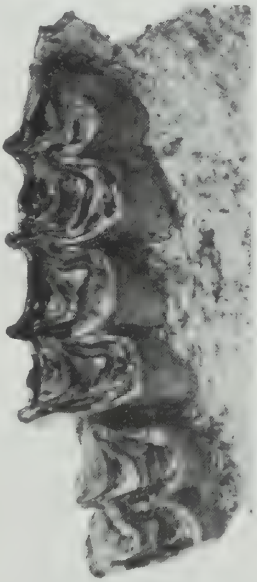

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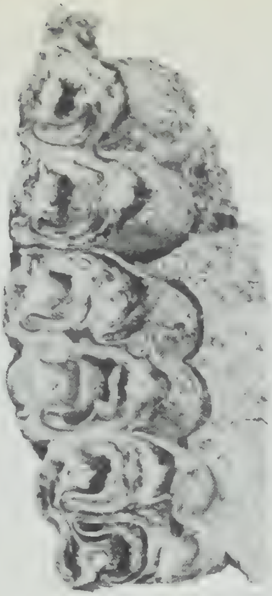

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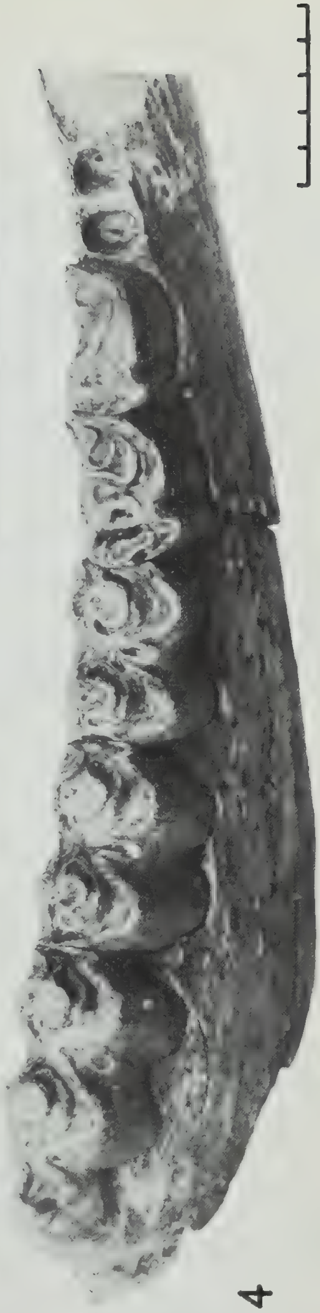

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Plate 1 (Scale = 25 mm)

Occlusal views of dentitions.

Fig. 1 ***Tragelaphus strepsiceros maryanus.*** Right mandible with P_2–M_3, FLK I G.067/1100.

Fig. 2 ***Tragelaphus strepsiceros maryanus.*** Left M^1–M^3 from palate, FLK I C.067/1083.

Fig. 3 ***Syncerus acoelotus.*** Left M^1–M^3, BK II 1963.2757.

Fig. 4 ***Syncerus acoelotus.*** Right mandible with P_3–M_3, BK II 1953.067/5230.

than in the living greater kudu, and a complete right lower dentition FLK I G.067/1100 also differs in having rather a short premolar row (Fig. 2; Pl. 1, fig. 1). Since this character is known from only one specimen we have not included it in the subspecific diagnosis. The paraconid–metaconid fusion on P_4 is known from five *T. s. maryanus* (two in late wear) and is just beginning on a further two in middle wear. This contrasts with its occurrence in only 13 out of 24 extant greater kudus and 3 out of 7 lesser kudus. Part of a right maxilla HWK EE II 1972.3916 has preserved its M^2 and M^3, the former having an occlusal length of 21·9 mm. This fits *T. s. maryanus* but is rather small for later greater kudus. If it is really *T. s. maryanus* then the range of the subspecies extends into lower middle Bed II.

Most of the tragelaphine limb bones from Bed I seem too small to belong to *T. s. maryanus* (Fig. 3). However, no other tragelaphine is known by cranial and dental remains and the alternative supposition that the postcranial remains alone represent another species is also hard to accept. The limb bones are discussed further in the account of the FLKNN I site.

Olduvai kudu specimens in London include three pieces possibly of *T. s. maryanus*. They are part of a right horn core M 21478 found in Bed I or II in 1947, the distal part of a left horn core M 21483, and the base of a left horn core M 21485.

MEASUREMENTS. Measurements on crania of *T. s. maryanus* are:

	Holotype	KK 068/5813
Anteroposterior diameter at base of horn core	76·5	73·7
Mediolateral diameter at base of horn core	55·4	56·9
Minimum width across lateral surfaces of horn pedicels	*c.* 119·0	–
Maximum braincase width	119·7	122·0
Skull width across mastoids immediately behind external auditory meati	*c.* 150·0	150·0
Occipital height from top of foramen magnum to top of occipital crest	58·6	58·7
Width across anterior tuberosities of basioccipital	36·4	–
Width across posterior tuberosities of basioccipital	54·2	61·0

Measurements on maxillae assigned to *T. s. maryanus* are:

	DK I 802	FLKNN I 553	FLK I C.067/1083
Occlusal length M^1–M^3	65·5	66·2	70·8
Occlusal length M^2	23·7	22·1	24·3
Occlusal length P^2–P^4	–	46·8	–

An immature maxilla FLK I G.067/1089 has deciduous P^2–P^4 at 50.0 mm.

Measurements on mandibles assigned to *T. s. maryanus* are:

	DK I 36	DK I 3001	FLKNN I 66+548	FLKNN I 62	FLK I G.067/1100	FLKN I 882
Occlusal length M_1–M_3	72·7	74·0	70·9	–	72·1	69·4
Occlusal length M_2	23·1	22·3	21·5	–	22·8	23·3
Occlusal length P_2–P_4	–	–	–	42·9	43·9	–

An immature mandible FLK I G.067/1085 has deciduous P_2–P_4 measuring 46·1 mm. It belongs to the same individual as immature maxilla G.067/1089. Maxilla FLKNN I 553 and mandibles 62 and 66 + 548 belong to one individual.

Measurements of length and least thickness on the limb bones, which are rather small for *T. s. maryanus*, using the reference points given in the introduction, are:

Metatarsals	DK I 4429	213 × 20·5	FLK I G.067/959	207 × 20·5	FLKN I 7333	220 × 25·6
Radii	FLKN I 8275	217 × 28·8	FLKN I 9290	224 × –		
Metacarpals	DK I 4141	218 × 21·8	FLKNN I 895	224 × 25·0	FLKN I 9269	223 × 23·0
	FLKN I 067/1073	222 × 25·3				

Measurements on two limb bones of a larger tragelaphine are:

Femur DK I 5400 330 × 33·5 Metacarpal FLK I G.258 238 × 29·0

COMPARISONS. Other fossil kudus are considered under *Tragelaphus strepsiceros grandis*, p. 303. The subspecies *T. s. maryanus* has not been discovered at any site other than Olduvai.

Tragelaphus strepsiceros grandis (L. S. B. Leakey 1965)

1965 *Strepsiceros grandis* Leakey : 38, pls 38–39.

DIAGNOSIS. A subspecies of *Tragelaphus strepsiceros* differing from the living greater kudu in its greater size; horn cores with greater basal divergence, less mediolateral compression and a more triangular cross-section; braincase widening towards the rear in dorsal view. It differs from *T. s. maryanus* by its larger size and in having horn cores with a more triangular cross-section and less mediolateral compression.

HOLOTYPE. A cranium with complete horn cores, BM(NH) M 21461, found in 1931.

HORIZON. The holotype is from upper Bed II. It came from RK (M. D. Leakey 1971b : 284). Other specimens are from middle Bed II to Bed IV at Olduvai, and from Peninj, but it is not abundant.

REMARKS. The holotype cranium is larger than large skulls of living greater kudu. Both its horn cores are complete and have strong anterior keels. Both horn cores show marks of the grubs of a moth allied to or identical with the living *Ceratophaga vastella* along the whole of their length[1].

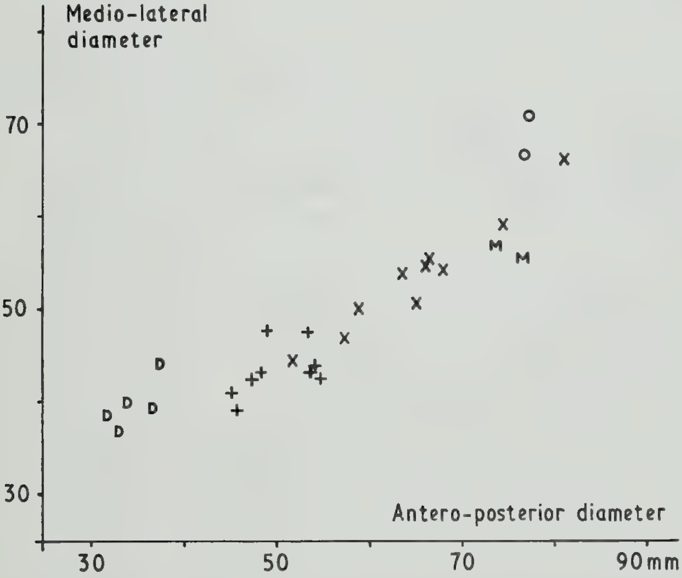

Fig. 4 Horn core dimensions of kudus.

O = *Tragelaphus strepsiceros grandis* from Olduvai Gorge, M = *T. s. maryanus* from Olduvai Gorge, + = *T. gaudryi* from member G of the Shungura Formation, X = living *T. strepsiceros*, D = *T. imberbis*.

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[1] A number of Olduvai fossil horn cores show grooves similar to those on dead modern antelopes made by grubs of the moth *Ceratophaga vastella* (Zeller) of the family Tineidae. The grubs feed on the keratin of the horn sheaths, having entered the space between the sheath and core at the base of the horn. They finally bore through the sheath to pupate in tubes of silk and detritus projecting from the sheath's external surface (Spinage 1962 : 81; pl. 36). In hot and dry regions the tubes form on the unexposed side of the horn sheath, making 'roots' into the ground (R. H. Carcasson, personal communication). Fossils showing signs of the grubs must have been lying in the open, neither buried nor under water, for a short period prior to fossilization. Leakey (1965 : 39, 51 and 62) has attributed some examples of such grooves to the gnawings of large rodents.

The fossil differs from living greater kudu in having horn cores that are set widely apart, more divergent immediately at the base in anterior view, with less emphasized spiralling, and with a less reduced posterolateral keel giving the horn core a more triangular and less oval cross-section and hence less mediolateral compression (Fig. 4). It also has a shorter, wider and relatively lower cranium, posterior widening of the braincase in dorsal view and possibly a deeper depression in the side of the braincase which is visible on the right side only. Most of these differences are likely to arise from individual variation and allometry. It is probable that the large size of *T. s. grandis* produces a general widening of the skull and enlarging of the horn cores, but the width across the supraorbital pits does not seem to be affected (Fig. 5). We consider it only subspecifically distinct from the living greater kudu. The right maxilla of the holotype is preserved separately from the cranium and has a tooth row which is larger than in most greater kudus, despite being fairly well worn.

Kudu remains in London which could be *T. s. grandis* are part of a left horn core M 21476, part of a left horn core M 21477 from BK IV found in 1935, the base of a strongly divergent left horn core M 14549 found in 1932 in Bed I (according to its label), Bed II (written on the horn core and in the register) or the surface of Bed III (Leakey 1965 : 40), and parts of right horn cores M 21469 (said by Leakey 1965 : 40 to come from the surface of CK IV in 1935), M 21470 and M 21471. The distal part of a left horn core M 14517 found in 1931 in Bed I, a small part of a left horn core M 21479, part of a horn core M 21480 found in 1931, and part of a right horn core M 21481 are all of kudus but are too fragmentary to be assigned to a subspecies. Parts of left horn cores M 14543 from Bed I and M 21482 may belong to a kudu or to a sitatunga-like tragelaphine.

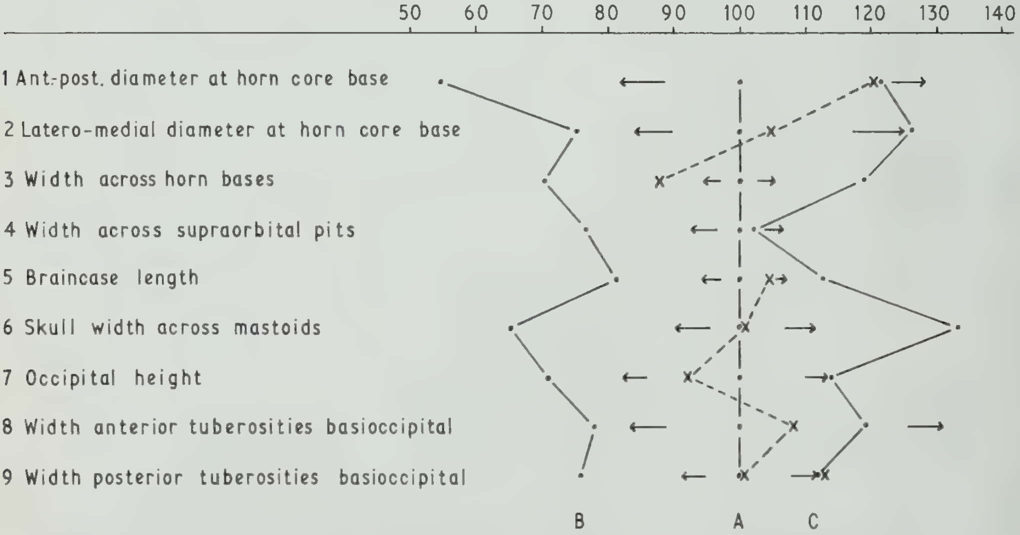

Fig. 5 Percentage diagram of skull measurements in kudus. Line A is the standard line at 100% ; readings on other lines are expressed as percentages of their values on line A.

A = mean readings for 10 adult males of living *Tragelaphus strepsiceros*, B = mean readings for 6 adult male *T. imberbis*, C = holotype of *T. strepsiceros grandis*, dashed line = holotype of *T. s. maryanus*.

Horizontal arrows show the standard deviations for line A. Braincase length is measured from the midfrontals' suture at the level of the supraorbital pits to the occipital top. *T. s. grandis* differs from the living greater kudu by being larger and having large horn cores set widely apart and a relatively low and wide occipital surface. *T. s. maryanus* shows strong mediolateral compression of the horn cores, which is probably responsible for the low reading of width across the horn bases. The relatively long and high cranium of the lesser kudu, B, is probably an effect of allometry, and this species also has mediolaterally wide horn cores.

T. strepsiceros subsp. Schwarz (1937 : 30) at Olduvai was based on a poorly-preserved frontal with horn cores which was unfortunately destroyed in Munich during the Second World War. Schwarz did not figure the specimen.

MEASUREMENTS. Measurements on the cranium and maxilla of BM(NH) M 21461 are:

Length of horn core along its front edge	*c.* 730·0
Anteroposterior diameter of horn core at its base	76·9
Mediolateral diameter of horn core at its base	66·6
Minimum width across lateral surfaces of horn core pedicels	161·0
Width across lateral edges of supraorbital pits	69·3
Maximum braincase width	135.5
Skull width across mastoids immediately behind external auditory meati	198·0
Occipital height from top of foramen magnum to top of occipital crest	72·5
Width across anterior tuberosities of basioccipital	40·0
Width across posterior tuberosities of basioccipital	60·5
Occlusal length M^1–M^3	81·7
Occlusal length M^2	*c.* 28·0
Occlusal length P^2–P^4	*c.* 50·0

COMPARISONS. A kudu-sized tragelaphine is represented at Peninj by fragments of two left maxillae A67.276 (WN 64.70 MMG.BSC) and A67.275 (WN 64.98 MMG.BSC), two pieces of a right mandible with P_4–M_3 A67.270 + A67.277 (WN 64.91 LMG.BSC.OG), the proximal end of a right metatarsal A67.346 (WN 64.420) and possibly some other pieces. We no longer believe that more than one tragelaphine is present (cf. Gentry *in* Isaac 1967 : 252). By the length of the mandibular molar row it agrees best in size with *T. s. grandis*, being a little small for an eland but rather too large for a living greater kudu.

The base of a right horn core from Kagua, BM(NH) M 15874, apparently the basis for Hopwood's (*in* Kent 1942 : 124) identification of *Taurotragus oryx*, is actually *Tragelaphus strepsiceros*. With basal diameters of 70·5 and 61·1 mm it has insufficient mediolateral compression to fit *T. s. maryanus*. It lacks the posterolateral basal keel of *T. s. grandis*. M 15884 is a small part of a kudu horn core from Kanam West. A tragelaphine left lower molar from Kanam Central, M 15933, is the size of a kudu.

A piece of horn core from the Shungura Formation, L.627-17 from member G, appears from its large size to belong to *T. strepsiceros* and is the only definite record of this species in the formation. Another kudu is common in members E to G, and was referred to *T. imberbis*, the lesser kudu, by Arambourg (1947 : 432; pl. 30, fig. 6). Its affinities are interesting. It differs from Olduvai *T. s. maryanus* and the living greater kudu by its smaller size and in having horn cores spiralled more closely to the longitudinal axis, less mediolaterally compressed at the base, less divergent overall and less uprightly inserted, braincase not widening posteriorly, and occipital surface perhaps less low and wide. The bending of the braincase on the face axis is about as strong as in *T. s. maryanus*. Passing from members E to G the anterior keel becomes stronger, the posterolateral keel weaker and mediolateral compression increases. These are all trends towards *T. strepsiceros* and away from *T. imberbis*, but the Omo kudu is unlikely to be ancestral to the Olduvai kudus. A change to *T. s. maryanus* would involve mainly a size increase with the associated changes of shortening and widening the braincase and the horn core insertions becoming more upright. However, the time margins are barely adequate according to the K-Ar dates of about 1·8 million years for Shungura tuff I_2 and about 1·9 million years for the Bed I basalts at Olduvai. *T. strepsiceros* must also have been a separate lineage, since the horn core L.627-17 occurs in the same level of member G (unit 13) as the highest horn cores of the other kudu. A cranium from Shungura member C, Omo 18 68-303, differs from the member E–G material by its slightly larger size, the weaker spiralling of its horn cores, their greater anteroposterior compression and a stronger posterolateral keel, all of which are satisfactory as ancestral character states. However, it also differs in the greater divergence of its horn cores, so that for this character it is the earlier rather than the later Shungura form which is most like *T. strepsiceros*. It is apparent that the member C cranium must be near the ancestry of both living kudus. We suggest that *T. strepsiceros* evolved from a form something like the member C cranium, but which is largely unrepresented in the Shungura Formation, and that the member E–G kudu also evolved from it. The Shungura E–G form lessened the divergence of its horn cores and perhaps diminished in size, but otherwise continued to evolve towards a *T. strepsiceros*-like morphology. By level 13 of member G, *T. strepsiceros* had appeared or reappeared in the Omo area, as witnessed by the horn core L.627-17, and we hypothesize that the Shungura kudu might then have reversed its remaining evolutionary parallels with *T. strepsiceros* and evolved into the living *T. imberbis*. Tragelaphine teeth of appropriate size for this lineage occur in higher member G and in member H, but as yet there are no horn cores. The chief motives for accepting this story are that *T. imberbis* and the Shungura species are similar-sized kudus occurring in the same region of Africa, the living one with no other known ancestor and the fossil one with no other known descendant. The outstanding interest of the story would lie in the implication that competition with a 'sister species' had led to the reacquisition of some ancestral horn core characters. Why should the species have benefited, or perhaps even been enabled to survive, by doing this?

Palaeoreas gaudryi Thomas (1884 : 15; pl. 1, fig. 7) was founded on a right horn core base (wrongly illustrated as a left) of a kudu from Ain Jourdel, an Algerian site of 'Villafranchian' (=Pliocene) age (Arambourg 1970 : 8). Joleaud (1936 : 1184) mistakenly referred *P. gaudryi* to *Taurotragus*. The horn core has an anterior keel and anteroposterior and mediolateral basal diameters of 48·8 and 47·4 mm. It is too small and has insufficient mediolateral compression for *T. s. maryanus*, but agrees with the Shungura E–G kudu in size, compression and inclination. Accordingly the latter can be referred to *Tragelaphus gaudryi* (Thomas) for the present, but it may be that the cladistic position of the Algerian form lies between the Omo member C cranium and *T. strepsiceros*. The type species of *Palaeoreas* is a small Miocene ovibovine (Gentry 1971 : 289) unconnected with the north African horn core. Another 'Villafranchian' kudu is a frontlet from Mansoura near Constantine, Algeria (Gervais 1867–69 : 92, 94; pl. 19, fig. 4), which is probably conspecific with the earlier Ain Jourdel horn core. Its spiralling lies fairly close to the longitudinal axis of the horn core, as in the Shungura kudu.

Horn cores of what appears to be a still earlier kudu occur in the Mursi Formation, Ethiopia (YS 4-4, 4-6, 4-10, YS 68-2078), and in the Karmosit beds in the Baringo area, Kenya (KNM-KM 13). They are more anteroposteriorly compressed and have a sharper posterolateral keel than in the Shungura E–G kudu, and these characters can be accepted as primitive. The horn cores agree with kudus in their increasing divergence from the base, which means that quite small pieces from any part of the horn core have the posterolateral keel along the concave edge of the curvature instead of the convex edge. This is in contrast to known members of other *Tragelaphus* lineages, but it would be premature to assume that such an early species can be related only to kudus.

The main features of skull evolution in the greater kudu can thus be taken as increasing mediolateral compression of the horn cores, increasing prominence of the anterior instead of the posterolateral keel and the horn core insertions becoming more upright. Connected with the overall increase of size, there was a shortening and widening of the braincase, and its roof acquired a less pronounced slope. The common kudu of the Shungura Formation is not an ancestor, and difficulties with *T. s. maryanus* are presented by the short premolar row of the only complete kudu-sized dentition from Bed I and by the greater proportion of P_4s with fused paraconid and metaconid than in living kudus.

Tragelaphus strepsiceros is represented by parts of two right horn cores, BM(NH) M 12147 and M 12904, at Broken Hill, Zambia, as noted by Leakey (*in* Clark 1959 : 229).

Fossil kudus are known from South African sites. At Makapansgat Limeworks, three tragelaphine species (other than the eland represented by maxilla BPI M.7) can be separated by the size of their teeth. The largest size group would correspond to larger examples of greater kudu and has been designated *Strepsiceros* cf. *strepsiceros* by Wells & Cooke (1956 : 9). It is represented by right maxillae BPI M.2 and M.3, left mandibles M.6446 and M.6690, immature right maxilla M.576 and immature left mandible M.4. More material is needed before deciding whether this tragelaphine might be *T. s. grandis*.

Remains of a distinctive extinct kudu occur at Melkbos and Elandsfontein, the Melkbos material having already been referred to by Hendey (1968 : 108). The horn cores of this species agree more with the greater than with the lesser kudu, but the spiralling is much tighter. The fossils perhaps represent a Cape species completely unknown in East Africa.

We now consider that the two pieces of horn core L.4615 and L.6586 from Langebaanweg which were recorded as a kudu by Gentry (*in* Hendey 1970a : 114) are more likely to be bovine.

Tragelaphus aff. ***scriptus*** (Pallas 1766)

There is some evidence for a bushbuck-like antelope at Olduvai. The distal end of a left horn core BM(NH) M 14568 from Bed IV (according to the register and by its colour; 'Bed I' on its label must be mistaken) is about the size of large horn cores of the living bushbuck, is anteroposteriorly compressed to the right extent and has an anterior keel and marked posterolateral keel. The anterior keel, however, is sharper than in most living *T. scriptus*. The distal end of a left tibia from SHK II, 1957.474 in Nairobi, is from a bushbuck-sized tragelaphine.

The frontal with horn cores called *T. scriptus* subsp. by Schwarz (1937 : 26) was destroyed in Munich in the Second World War. The specimen was not figured.

COMPARISONS. A pair of bushbuck-sized tragelaphine horn cores, L144-1 and 2 from member C of the Shungura Formation, Omo, is extremely interesting in that the horn cores are less anteroposteriorly compressed, less obliquely inclined in side view and possibly inserted less far behind the orbits than in the living bushbuck. The Makapansgat Limeworks dentitions assigned to *Cephalophus pricei* by Wells & Cooke (1956 : 12, fig. 5) belong to a bushbuck-sized tragelaphine.

Tragelaphus aff. ***spekei*** Sclater 1864

A skull with horn core from Olduvai was named *Tragelaphus spekei stromeri* by Schwarz (1932 : 2; 1937 : 28). It was formerly housed in Munich, but was lost during the Second World War. Schwarz described the horn core insertion as being further forward on the skull than in the living sitatunga, above the orbit instead of just behind, but did not figure the specimen. The anterior keel of the horn core was very marked. Parts of left horn cores, BM(NH) M 14543 from Bed I and M 21482, may belong either to a kudu or to a sitatunga-like antelope. The anterior keel is well marked on M 14543, which may be from near the distal end, but not on M 21482. There is no further evidence for a sitatunga at Olduvai, and we shall abandon the use of the name *T. spekei stromeri*.

COMPARISONS. Other fossils of sitatunga size are known from other African sites. The badly preserved cranium of *Tragelaphus* sp. cf. *buxtoni* from Laetolil (Dietrich 1942 : 118; pl. 19, fig. 154) was thought to have come from the early fauna, but this is not so (M. D. Leakey *et al.* 1976 : 463, 464). The rather open spiralling of its horn cores is the only reason for linking it with the living *T. buxtoni*; the oblique insertion of the horn cores is unlike *T. buxtoni*, and either *T.* sp. cf. *spekei* or *T.* sp. cf. *angasi* would have been better designations. Its horn cores are somewhat anteroposteriorly compressed, a posterolateral keel but not an anterior one is present, and the frontals are uparched between the horn core bases. Dietrich (1950 : 43) referred to another sitatunga- or nyala-sized horn core from Laetolil and to an appropriately-sized mandible.

BM(NH) M 26402 is a right horn core from the earlier fauna of the Kaiso Formation at North Nyabrogo described by Cooke & Coryndon (1970 : 200) as *Strepsiceros* cf. *maryanus*, but better identified as *Tragelaphus* sp. cf. *spekei*. It is less tightly twisted and a little less anteroposteriorly compressed than in *T. spekei*, but does not seem very primitive for its great age. It is unlikely to be a kudu because of the strong posterolateral keel, absence of an anterior keel at least lower down and the poor degree of twisting. Part of a left horn core from Kanam East M 15907 is also less anteroposteriorly compressed than in *T. spekei*. Part of a left horn core from Kanam East Hot Springs M 15929 is similar but has a stronger anterior keel. Part of a left mandible with M_2 and M_3, M 15924 from Kanam East, is too large for a bushbuck and shows larger basal pillars than in living Tragelaphini. A right mandible from Rawe M 15938 is the size of *T. spekei*. Three horn core pieces from Kanjera M 15852 (*Tragelaphus* sp. of Hopwood *in* Kent 1942 : 126) are also of sitatunga size and closer to the living species; they have poor or absent anterior keels. The base of a tragelaphine right horn core BPI M.490 and possibly a fragment M.491 from Makapansgat Limeworks show rather less anteroposterior compression than in the Kaiso horn core. Some dentitions of appropriate size to go with them have already been assigned to *T.* cf. *angasi* by Wells & Cooke (1956: 10). These are right maxilla M.5, right mandible M.6606, left mandible M.6, right M_2+M_3 M.183, left M_3s M.185 and M.186, and probably right maxilla M.1319. Very similar remains are fairly common in the Langebaanweg collection.

Genus ***TAUROTRAGUS*** Wagner 1855

Type species. *Taurotragus oryx* (Pallas 1766).

Generic diagnosis. Large tragelaphines. Compared with *Tragelaphus* the horn cores are tightly twisted and less openly spiralled, inserted wider apart, and with a strong anterior keel and sometimes a posterolateral one. Large supraorbital pits; pronounced lateral flanges at the front of the nasals; median indentation at the back of the palate passing far forwards of the lateral ones; tooth rows set more anteriorly than in *Tragelaphus*; P_4s with fused paraconid and metaconid (unfused in only 2 out of 27 *Taurotragus oryx*).

Taurotragus arkelli L. S. B. Leakey 1965

1965 *Taurotragus arkelli* Leakey: 43, pls 43 and 44.

Diagnosis. A species of *Taurotragus* differing from living *T. oryx* in having horn cores inserted less obliquely in side view, braincase top longer, cranium high and narrower, and the braincase top not depressed to produce a transverse crest across the top of the occipital.

Holotype. Cranium with complete left and basal half of the right horn core, F.3665 P.P.T.4 found in 1941. At present in the Nairobi collections.

Horizon. The holotype was found on the surface of Bed IV, between LK and RK. Apart from this the eland is poorly represented at Olduvai.

Remarks. The single cranium of *T. arkelli* is a little smaller than crania of the living eland and the horn cores are inserted less obliquely and perhaps closer to the orbits. The supraorbital pits are rather close together. Other differences from living *T. oryx* are connected with the less oblique insertions of the horn cores; these are the longer braincase top (Fig. 6), no temporal fossa, and

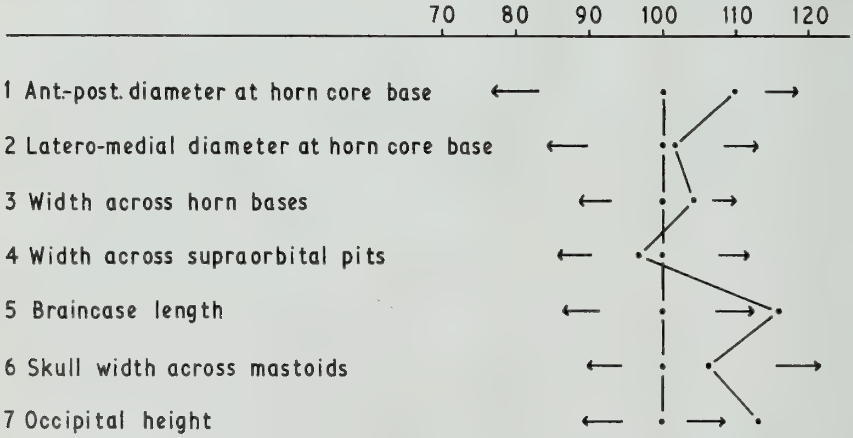

Fig. 6 Percentage diagram of skull measurements in elands. Braincase length is measured as in Fig. 5. The standard line at 100% is the mean of 12 living *Taurotragus oryx*, and standard deviations are also shown. The second line is for the holotype of *T. arkelli*, which has a longer and higher cranium, and supraorbital pits rather closer together than in *T. oryx*. The mediolateral compression of its horn cores may not differ much from large individuals of the living species.

no sinking of the braincase roof behind the horn cores to leave a narrow transverse crest across the top of the occipital. This last feature causes the angle of the parietal surface with the occipital to be more than 90° in the fossil, whereas it is less than 90° in the living species, as was noted by Leakey (1965 : 43). Other features seen on the cranium are typical of the living species: the long top edge of the occipital, the very poor median vertical ridge on the occipital with no flanking hollows, the long basioccipital and the large foramina ovalia. The size of the mastoid exposure is uncertain; it is certainly not larger on the occipital surface than in the living eland but the anterolateral edge is not clear. The horn cores of *T. arkelli* are short and not as divergent as in some individuals of extant west African and Sudanese populations called *T. oryx derbianus* and *T. o. gigas*. There is a weak posterior keel on the horn cores, and both the anterior and posterior keels are present to the tip of the left horn core.

Other remains of *Taurotragus* from Olduvai are part of a right horn core BM(NH) M 29415 from the surface of Bed II in 1935 and a small part of a left horn core M 29414 from Bed IV. In Nairobi there is a nearly complete left horn core with part of the frontal WK IV 1970.3641 and part of a right horn core 068/5924 which was a surface find at the Gorge and lacks the posterior keel. Species determinations are impossible for these pieces. The cranium E-58 and other remains from Olduvai of *T. oryx pachyceros* Schwarz (1937 : 33) which were originally in Munich were destroyed during the war. It is unfortunate that Schwarz did not figure the specimens; nothing in his descriptions suggests that they could have been from *T. arkelli*, and we shall abandon the use of his name.

MEASUREMENTS. Measurements on the cranium F.3665 P.P.T.4 of *Taurotragus arkelli* are:

Length of horn core along its front edge	430·0
Anteroposterior diameter of horn core at its base	71·5
Mediolateral diameter of horn core at its base	62·9
Minimum width across lateral surfaces of horn core pedicels	160·0
Width across lateral edges of supraorbital pits	85·9
Maximum braincase width	121·0
Skull width across mastoids immediately behind external auditory meati	179·0
Occipital height from top of foramen magnum to top of occipital crest	77·7
Width across posterior tuberosities of basioccipital	64·7

COMPARISONS. There are parts of two other fossil *Taurotragus* horn cores in the Nairobi collections, both lacking a posterior keel. They are the distal end of a right horn core from the Pleistocene deposits at Songhor, Kenya, and the basal part of a right horn core 068/6414 from Chemeron Plio-Pleistocene beds, found in 1966, which is larger than the horn cores of *T. arkelli*. The eland recorded by Hopwood (*in* Kent 1942 : 124) from Kagua, Kenya, on a right horn core base BM(NH) M 15874 is actually a kudu.

The piece of horn core in Berlin from Laetolil assigned to *Taurotragus* sp. cf. *gaudryi* (Thomas) by Dietrich (1950 : 43; pl. 4, fig. 46) is certainly of *Taurotragus* and from the right side but seems unlikely to be from the older fauna. For more remarks on *T. gaudryi* see p. 304. The right maxilla with P^4–M^3 which was also assigned to *Taurotragus* sp. cf. *gaudryi* by Dietrich (1950 : 43; pl. 3, fig. 41) has molars with rounded medial lobes and outbowed ribs between the styles, and is in fact bovine. It is probably conspecific with the teeth assigned to ? *Simatherium kohllarseni* (Dietrich 1950 : 44; figs 5, 32 and 36).

Arambourg (1947 : 434) referred to a large lower molar from the Shungura Formation, Omo, which he thought belonged to *Taurotragus*, and there is a mandibular fragment, P996-55, from member K as well as a molar fragment, Omo 28 68-2496, from member B, both of large size.

Eland fossils are fairly common at South African sites. A partial left maxilla BPI M.7 from Makapansgat Limeworks may be of a very large tragelaphine the size of *Taurotragus*; it was identified as *Taurotragus* cf. *oryx* by Wells & Cooke (1956 : 10). Cooke (1949 : 38, 44, 52) and Wells (1964b : 91) also listed *T.* cf. *oryx* from the Vaal River deposits, and Cooke & Wells (1951 : 205) recorded *T.* cf. *oryx* on teeth from Chelmer in Rhodesia.

Several crania and frontlets and many horn cores of *Taurotragus* occur at Elandsfontein. They are much closer to living *T. oryx* than to the Olduvai *T. arkelli* and the braincase tops are almost as short as in the living eland although the horn cores are perhaps more upright in their insertions. The Elandsfontein fossils would be younger than *T. arkelli* on the assumption that there has been but one lineage of *Taurotragus*. They illustrate very well the variability of the posterior keel on eland horn cores; it may be nearly absent, well-marked near the base, or well-marked from base to tip. It is better developed in males than females.

A piece of a juvenile right mandible and a large left lower molar from Florisbad may represent eland.

A frontlet with complete horn cores SAM Mb 70, a horn core fragment Mb 589 and parts of two mandibles Mb 10 and Mb 11 from Melkbos are of *Taurotragus oryx* (Hendey 1968 : 109). In Bloemfontein a cranium with complete horn cores C.2738 from Knoffelsvlei, Middelburg, and a frontlet with complete horn cores C.2797 from Mazelspoort are indistinguishable from the living eland.

Taurotragus oryx is common at Broken Hill, Zambia, as indicated by Leakey (*in* Clark 1959 : 229). The partial frontlet with left horn core BM(NH) M 12906 shows that it was more advanced than *T. arkelli*.

An eland is known from the later Pleistocene of north-west Africa, but disappeared at the start of the Holocene (Arambourg 1962 : 107). Arambourg (1938 : 42) referred to teeth from Ain Tit Mellil and El Khenzira in Morocco and figured a frontlet (pl. 9, fig. 3) from Casablanca. There is no evidence that these remains, nor a horn core from Pointe Pescade, Algeria (Pomel 1895 : pl. 7), are not the living species. Nothing in the illustrations or descriptions suggests they could be *T. arkelli*. However, the eland reported from the earlier site of Ternifine, Algeria (Arambourg 1962 : 106), is most unlikely to be of the living species.

Tribe **BOVINI**

This tribe comprises the late Tertiary to present-day descendants of different lineages of boselaphines. They are usually large and have low and wide skulls. The cranial features are: horn cores inserted at varying distances behind the orbits, without transverse ridges but sometimes with a very weak torsion, present in both sexes in living forms, frontals hollowed internally, the horn cores also internally hollowed in living species, preorbital fossae weak or absent, braincase shortened, infraorbital foramen tending to be low and anteriorly placed on the skull, basioccipital triangular in shape, molars with basal pillars and complicated central cavities, upper molars with prominent ribs between the styles, lower molars without large goat folds.

Among the living bovines, the cattle of Eurasia (*Bos* spp.) have wide frontals with horn core insertions set widely apart and so far back as to overhang the occipital, and have long faces. Bison of North America and Eurasia (*Bos bison* and *B. bonasus*) have wide skulls and short faces, and the short horn cores are inserted further forwards than in cattle but still behind the orbits. All species of *Bos* possess ethmoidal fissures, at least until the earlier part of adult life. Water buffaloes of southern Asia (*Bubalus arnee*) have long faces, very long and keeled horn cores inserted just behind the orbits, and a vomer fused to the back of the palate. There are also some smaller island forms of *Bubalus*. African buffaloes (*Syncerus caffer*) are short-faced and have horn cores inserted just behind the orbits. The horn cores are short and populations from east and southern Africa have enlarged basal bosses. The paraconid and metaconid on P_4 are generally fused. Among extinct genera, *Leptobos* Rütimeyer is clearly related to *Bos*, and *Proamphibos* Pilgrim and *Hemibos* Falconer to *Bubalus*.

In later Pleistocene deposits of Africa there are found large bovines generally similar to *Syncerus* but differing from it in their larger size, and in having long and less dorsoventrally compressed horn cores without basal bosses. Bate (1949) founded the genus *Homoioceras* for these buffaloes and (1951) recognized the following species:

Homoioceras singae Bate 1949, based on a skull with horn core bases from Singa on the Blue Nile, Sudan, and other fragments from the nearby site at Abu Hugar. This is the type species.

H. antiquus (Duvernoy 1851), from many sites in north-west Africa, mainly Algeria, well illustrated by Pomel (1893).

H. baini (Seeley 1891), from many sites in South Africa.

H. nilssoni (Lönnberg 1933), known only from a complete skull and skeleton from the River Melawa, near Naivasha, Kenya. The specimen is now in Stockholm. Its cheek teeth show considerable occlusal complexity.

It is important to reiterate Miss Bate's conclusion that these long-horned buffaloes resemble *Syncerus* and not *Bubalus*. They agree with *Syncerus* and differ from *Bubalus* in their shorter faces, keels not always present on the horn cores and frequently neither regular nor persistent, short nasals without lateral flanges anteriorly, premaxillae with only a short or no contact on the nasals, vomer not fused to the back of the palate, a lower and wider occipital, and a paraconid–metaconid fusion or approach to it on P_4. There are some limb bone similarities between *Syncerus caffer* and the skeleton of *Homoioceras nilssoni*, but it is not possible to ascertain differences from *Bubalus*, of which only one postcranial skeleton of *B. arnee* and one of the much smaller *B. depressicornis* are available in London. It is unfortunate that the holotype skull of *H. singae* most probably belongs to a short-horned buffalo, as was first suggested to us by J. W. Simons, and that the generic name *Homoioceras* is therefore a junior synonym of *Syncerus*.

A further large extinct African bovine is *Pelorovis oldowayensis* and its synonym *Bularchus arok*. The species was first described by Reck (1928) from Olduvai Gorge, and is not known outside East Africa. Reck had thought that his original cranium with horn cores belonged to a giant member of the Caprini, distantly related to sheep. However, one of the more striking later finds at Olduvai was a herd of *P. oldowayensis* at BK II in 1952 (Leakey 1954). It became clear from a study of this herd that *P. oldowayensis* is a bovine with an impressive number of resemblances to '*Homoioceras*' (Gentry 1967 : 287). The chief differences from '*Homoioceras*' are that the horn cores of *P. oldowayensis* are inserted close together and very posteriorly, passing backwards from their insertions then outwards, the face is longer, the tooth rows set more anteriorly and the occlusal pattern of the cheek teeth is simpler.

This assessment of *P. oldowayensis* was based on a comparison with the skeleton of '*H.*' *nilssoni*, the holotype cranium and Pomel's illustrations of '*H.*' *antiquus*, and a cast of the skull of *H. singae*. We have now seen much South African material of '*H.*' *baini*. The holotype in Cape Town is a cranium with horn cores, from alluvial deposits of unknown age of the Modder River, Orange Free State. There are also other remains from Cornelia, Florisbad and Vlakkraal in the National Museum, Bloemfontein. Those from Cornelia are an unnumbered face with tooth rows, a left maxilla C.918, a right mandible C.918 and a right M_3 C.2857; those from Florisbad are a right maxilla C.1476, part of a left mandible C.2902, and two unnumbered left and right upper molars, and from Vlakkraal there is a cranium C.1538 with long horn cores without basal bosses. Finally, Cooke & Wells (1951 : 205, fig. 1) described an upper tooth row from Chelmer, Rhodesia. The occlusal pattern of the molars of '*H.*' *antiquus* and the Cornelia and Chelmer '*H.*' *baini* is slightly less complicated than in '*H.*' *nilssoni*. The Florisbad animal is slightly smaller and has similar teeth and a mandible which is not very deep below M_3.

The Elandsfontein material in the South African Museum, Cape Town, may be the best existing collection of long-horned buffaloes. Many of the cheek teeth, especially those in earlier wear, have markedly simple occlusal surfaces. This is manifested in small basal pillars, a simple outline of the central cavities, little outbowing of the ribs between the styles on the upper molars and a less 'pinched in' appearance of the lateral lobes of the lower molars. In later wear they appear to be as advanced as at other sites, but not to match the complexity seen in '*H.*' *nilssoni*. Furthermore, the premolar row is unusually long, and there is practically never any paraconid–metaconid fusion on P_4, whereas in other '*Homoioceras*' this occurs in later wear. There are few other differences except perhaps flatter nasals, a less deep zygomatic bar below the orbit and narrower anterior tuberosities of the basioccipital. The somewhat simplified occlusal morphology of the cheek teeth in the Elandsfontein buffalo weakens the generic difference between '*Homoioceras*' and *Pelorovis*. It thus seems best to place all the extinct long-horned bovines of Africa in one genus *Pelorovis*. There are two species, *P. oldowayensis* for the animal first described from Olduvai, and *P. antiquus* for the other fossils. Further, more detailed work may show the trivial names *baini* and *nilssoni* to have continuing usefulness at subspecies level. Our supposition is that *P. antiquus* is closer to *P. oldowayensis* than to short-horned buffaloes of the *Syncerus* lineage, and may be the descendant of *P. oldowayensis*.

Genus *PELOROVIS* Reck 1928

1928 *Pelorovis* Reck : 57.
1936 *Bularchus* Hopwood : 639.

Type species. *Pelorovis oldowayensis* Reck 1928.

Generic diagnosis. Extinct large African bovines with massive, long, curved horn cores, slightly compressed dorsoventrally and without keels; both sexes with horns; frontals hollowed internally; no ethmoidal fissures; no preorbital fossae; premaxillae either not reaching the nasals or having only a short contact; nasals fairly short; vomer not fused to the back of the palate; occipital low and wide; P_4s with paraconid and metaconid growing close together and usually fusing in late wear.

Horizon. From the Shungura Formation, Omo, surviving until the end of the Pleistocene.

Remarks. *Homoioceras* is not placed as a synonym because the type species is based on a *Syncerus* specimen (p. 309). However, *Pelorovis* includes all other species formerly referred to *Homoioceras*.

Pelorovis oldowayensis Reck 1928

1928 *Pelorovis oldowayensis* Reck : 57, text-fig. 1; pls 1 and 2.
1936 *Bularchus arok* Hopwood : 639, no figure.

Diagnosis. Horn cores not hollowed internally, inserted close together and so far posteriorly as frequently to overhang the occipital surface, curved backwards from the base, then outwards and finally forwards and a little upwards; nasals domed transversely; anterior part of the zygomatic arch thickened below the orbits; anterior tuberosities of the basioccipital rather wide apart for a bovine; molars with small basal pillars and central cavities simple in outline; upper molars with poorly localized and outbowed ribs between the lateral styles; mandibles with deep horizontal rami.

Holotype. A cranium with horn cores in Berlin, field numbers 1516, 1517 and 1518.

Horizon. The holotype was found on the north side of the Gorge near the human burial at the site now known as RK. Dietrich (1933 : 299) wrote that it came from Bed IV. The species is plentiful at Olduvai, but the other remains are all from middle and upper Bed II except for a mandible and a tooth from Bed III. The species is also known from Kanjera and probably from the Shungura Formation, Omo.

Remarks. Gentry (1967) listed material from SHK II and BK II at Olduvai, including two complete skulls from the latter site. Material from other sites was less plentiful, and consisted of a left mandibular fragment and a distal metatarsal from MRC II, a right astragalus 1959.211 from KK II, a distal metacarpal 1957.367 from the surface of FC II and a seventh cervical vertebra from an unknown level at HWK II. Teeth have subsequently been found at MNK II and in the highest levels of HWK East II (Pl. 11, fig. 1). Part of a left mandible BM(NH) M 29460 comes from Bed III and was probably found in 1931 ('III' is written on it with the yellow ink used on several 1931 fossils); P_3–M_3 are present in early wear but with extensively cracked enamel walls, and have quite a simple occlusal pattern which fits *P. oldowayensis*. On P_4 the metaconid is growing towards the paraconid, but fusion has not yet occurred at this early stage of wear. A right upper molar, JK III/4, 1969.607, also fits *P. oldowayensis*.

Gentry (1967 : 290) discussed the hypodigm of *Bularchus arok* Hopwood, and decided that it was the same species as *Pelorovis oldowayensis*. The holotype frontlet, BM(NH) M 14947, probably came from PLK at the top of Bed II (M. D. Leakey, personal communication and 1971b : 283). Gentry (1967 : 291; pl. 5, figs 3 and 4; pl. 6) also discussed the second complete skull found with the BK II herd in 1952. Compared with the first, probably female, skull, it had longer horn cores which were more compressed, inserted less posteriorly and not overhanging the occipital, the zygomatic arch deeper anteriorly, the tooth row positioned less anteriorly (Fig. 7, readings 5 and 6), the occipital surface lower and wider, the anterior tuberosities of the basioccipital wider and the mandibular ramus slightly shallower. It seems better to accept this skull as lying within the

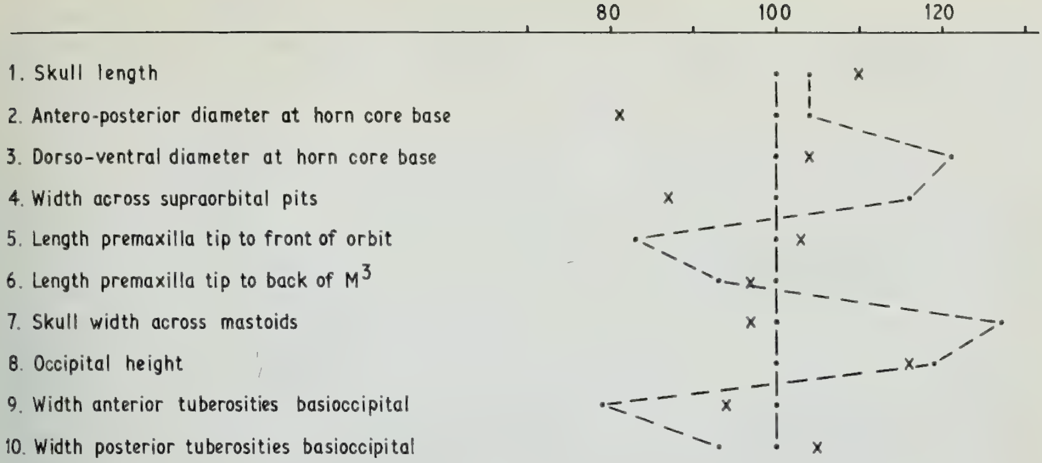

Fig. 7 Percentage diagram of skull measurements in Bovini. The standard line is for the BK II skull of *Pelorovis oldowayensis* which is probably a male; the second line is for the *P. antiquus* skull from Naivasha, Kenya. Crosses mark the readings for the supposed female skull of *P. oldowayensis*. The male *P. oldowayensis* has strong compression of its horn cores; *P. antiquus* has larger horn cores, a shorter face (readings 5 and 6), a very wide and relatively low occipital and narrow anterior tuberosities on the basioccipital.

range of variation of *P. oldowayensis* than to place it in a separate species, particularly as it was found in the same herd as the first skull. In many of its characters it shows signs of approach to *P. antiquus*, as in those of the horn cores, the position of the tooth row, the shallower mandible and the proportions of the occipital.

Comparisons. *Pelorovis oldowayensis* is known from Kanjera by a pair of mandibles BM(NH) M 15856 (referred to *Bularchus arok* by Hopwood *in* Kent 1942 : 126), a left upper molar M 25676, part of a left upper molar M 25688, part of a right upper molar M 25677, an incomplete left M_3 M 25692 and three tooth fragments M 25679–81 (Gentry 1967 : 291). There are also many horn core pieces.

Pieces of large curved horn cores from members D, F, and G of the Shungura Formation, Omo, may well belong to *Pelorovis*, if not to *P. oldowayensis*. They include L.16-(9 + 81) and L.16-101. A few bovine teeth from members C, E and F are large enough for assignment to *Pelorovis*, but are not morphologically distinguishable from *Syncerus*. This situation is a contrast to that with the bovine teeth of middle and upper Bed II at Olduvai.

The cranium of *Simatherium kohllarseni* Dietrich (1941 : 221; 1942 : 119; pl. 20, figs 161, 163 and 165) from the Vogel River, Laetolil, numbered Vo 670 in Berlin, is almost as large as *Pelorovis oldowayensis* and could be its ancestor. The horn cores are long, dorsoventrally compressed, strongly divergent, inserted obliquely in side view, and large in relation to skull size, all of which are resemblances to *P. oldowayensis*. There are three interesting differences: the horn cores are inserted less far backwards (well forwards of the level of the occipital surface), the insertions are wider apart, and the end of the left horn core, as preserved, is beginning to curve more backwards and less outwards. The first and last characters can reasonably be expected in an ancestral form; in fact it is noteworthy that the lessening divergence of the distal parts of the horn cores in *Simatherium* is closer to other primitive bovines such as *Proamphibos* and *Leptobos* than is *Pelorovis*. Dietrich himself linked the Laetolil cranium with *Parabos* Arambourg & Piveteau. The wide insertion of the horn cores in *Simatherium* is less obviously a primitive character, but we consider it is not suffiicient to remove the species from a possible ancestry to *Pelorovis*. Dietrich (1950 : 44; pl. 1, fig. 5; pl. 3, figs 32 and 36) assigned to ? *Simatherium kohllarseni* some teeth which do not differ from other early bovine teeth. To become *P. oldowayensis* they would have to increase in size without acquiring a more complex occlusal pattern.

Two horn core fragments from Langebaanweg, L.4615 and L.6586, may represent *Simatherium* or an allied genus. They are large and curved and L.4615 has a very prominent keel. This caused Gentry (*in* Hendey 1970a : 114) to identify the horn cores wrongly as kudus. Some of the bovine teeth at Langebaanweg are notably large.

Pelorovis antiquus (Duvernoy 1851)

1851 *Bubalus antiquus* Duvernoy : 597, no figure.
1891 *Bubalus baini* Seeley : 201, figure.
1933 *Bubalus nilssoni* Lönnberg : 28; pls 1–3.

DIAGNOSIS. A species of *Pelorovis* with horn cores normally curved fowards and downwards from the base, inserted widely apart and behind the orbits but less posteriorly than in *P. oldowayensis*; anterior part of the zygomatic arch not thickened below the orbits; face shorter and tooth row set less anteriorly than in *P. oldowayensis*; occipital surface low and wide; molars with larger basal pillars and central cavities more complicated in outline, and upper molars with more localized and outbowed ribs between the styles than in *P. oldowayensis*.

HOLOTYPE. A cranium with horn cores in the Institut de Paléontologie, Paris.

HORIZON. The holotype came from near Setif in the Department of Constantine, Algeria. Thomas (1881 : 119) named the site as Oued Bou Sellam, and Romer (1928 : 88, 109) quoted an opinion of Joleaud that it came from between the 30 and 15 metre terraces, and hence might be of Lower Monastirian (between Tensiftian and Soltanian) age, which would be an equivalent of the early part of the last glaciation. However, the 15 and 30 metre terraces, at least in Morocco, could lie within the time span from the Holstein to the early Eem interglacials (Butzer 1972 : 24). Thus the holotype may come from the Upper or Middle Pleistocene.

Thomas (1884 : 17–18; pl. 4, fig. 6) attributed to this species a horn core tip from deposits of Villafranchian-equivalent age at Mansoura, but we do not believe that one can be certain of the species identification for such a fragment. It is difficult to find convincing north African occurrences of *P. antiquus* before the Middle and Upper Pleistocene, and Pomel (1888 : 229) remarked in connection with a possible Lower Pleistocene record at Palikao (=Ternifine), Algeria, that it is more especially characteristic of later sites. We can be sure that this species nearly always occurs later than *P. oldowayensis*. At Olduvai Gorge it is known from upper Bed IV.

REMARKS. The species is represented at Olduvai by the greater part of a right horn core WK East IV 1970 A.2305 (5) (Pl. 4, fig. 1). When complete this horn core would not have been so long as some other specimens from other parts of Africa. It is compressed dorsoventrally, without clear keels or transverse ridges, is inserted immediately behind the orbit so that its front edge is level with the supraorbital pits, emerges transversely in dorsal view and only very slightly upwards in front view, and curves gently backwards. There is a very small supraorbital pit and no sign of a temporal ridge behind the horn base. The length along the front curve as preserved is *c*. 790 mm, the anteroposterior basal diameter 134 mm and the dorsoventral diameter *c*. 80 mm.

It is possible that *P. antiquus* descends from *P. oldowayensis*. The different course of the horn cores ensures a more stable distribution of their weight on either side of the skull and may be linked with the usual but not invariable decline in anterior thickening of the zygomatic arch in *P. antiquus*. (The East African individual called *nilssoni* still has a thickened arch.) Increasing the massiveness of horn cores with a backwards then outwards curvature would lead to mechanical problems which could be ameliorated by such a change in course. Perhaps the second complete skull of *P. oldowayensis* in the BK II herd shows the first signs of this with its insertions being less posterior. The low level of the horn core tips on this skull (Gentry 1967 : pl. 5, fig. 3) could have been an increasing impediment to eating and drinking, and hence another reason for an evolutionary change. The same individual also shows other characters like *P. antiquus* (p. 310). A less likely alternative is that *P. antiquus* descended from some mid-Pleistocene *Syncerus* like that of Olduvai Bed II. *P. antiquus* agrees with this *Syncerus* in the general course of the horn cores, the shape of their basal cross-section and the clear temporal ridges at the side of the braincase roof.

If *P. antiquus* did descend from *P. oldowayensis*, the transition seems likely to have occurred during the time span of Olduvai Bed IV according to the evidence of a *P. antiquus* horn core in upper Bed IV and the supposed provenance of the *P. oldowayensis* holotype in Bed IV. The transition need not have taken place in East Africa, and it is still not known that the improved teeth evolved synchronously with the horn core changes. A *P. oldowayensis* mandible BM(NH) M 29460 is known as late as Bed III, as has already been noted. Other bovine dentitions and individual teeth from Bed III as a whole are not quite as large as the teeth of *P. oldowayensis*, but have larger basal pillars, more marked indentations into the central cavities and perhaps stronger and more localized ribs on the lateral walls of the upper molars. It is best to leave them as *Syncerus* for the present, and to suppose that tooth size increased in that lineage between Bed II and Bed III. However, changes in the stratigraphical interpretation of Olduvai Gorge need affect only a few fossil pieces in order to upset this evolutionary picture.

COMPARISONS. Part of a large left mandible from Peninj is possibly *P. antiquus*. This is A67.282 (WN64.256.MPI) probably from the Moinik Formation overlying the Humbu Formation (Isaac *in litt.*). The localized outbowings of the medial walls and constricted lateral lobes of the molars are more advanced than in *P. oldowayensis*. The occlusal length of M_2 is 35·1, and of M_3 49·8 mm. Dietrich (1950 : 47, fig. 56) described what are evidently fragments of a *P. antiquus* skull from the 'young Pleistocene' of the Eyasi area, Tanzania.

P. antiquus is present at Broken Hill, Zambia, as was noted by Leakey (*in* Clark 1959 : 229). The material registered as BM(NH) M 12143 includes parts of more than one *P. antiquus* skull, as well as a piece of a rhinoceros. Leakey noted how much this material differed from the holotype of *Homoioceras singae* but did not question the latter's identity as a long-horned buffalo.

Bate (*in* McBurney & Hey 1955 : 282, fig. 39) recorded *Homoioceras* sp. on two horn core bases from the late Pleistocene of Wadi Derna, Libya. One of the horn cores is registered BM(NH) M 16619. A skull from Bizerta, Tunisia could be *P. antiquus* (Bate 1951 : 19) but has horn cores passing directly outwards from their bases instead of slightly forwards (Solignac 1924 : pl. 6, fig. 1). The horn core base from Kom Ombo, Sudan, of '*Bubalus*' *vignardi* Gaillard (1934 : 37; pl. 5, figs 1–2) was noted by Bate (*in* Arkell 1949 : 24; 1951 : 18) as not resembling any other buffalo. A cast of it in London, M 16688, looks like *Bos primigenius*. Churcher & Smith (1972 : 260) and Churcher (1972 : 62) found *Bos primigenius* at Kom Ombo but no definite *Pelorovis antiquus*.

Genus *SYNCERUS* Hodgson 1847

TYPE SPECIES. *Syncerus caffer* (Sparrman 1779).

GENERIC DIAGNOSIS. Moderate-sized to large African bovines with wide skulls and short faces; horn cores short to moderately long, dorsoventrally compressed, often with keels, and emerging transversely from just behind the orbits; females with horns; supraorbital pits fairly close together; occipital surface low and wide; molars with moderate-sized basal pillars and central cavities without such an extremely complicated outline as in *Bos*; upper molars without such pronounced ribs between the styles as in *Bos*; the occlusal complexity of the teeth increasing with increased body size; P_4 with paraconid and metaconid growing towards one another or fused.

The following characters, known only from the living species, are quite likely to be valid for the genus: nasals fairly short, without lateral flanges anteriorly, and in a plane nearly parallel to the tooth row giving the face quite a high profile; no ethmoidal fissures; no preorbital fossae; premaxillae with only a short or no contact on the nasals; vomer not fused to the back of the palate.

REMARKS. The genus contains two species, the type species *Syncerus caffer* and a new fossil species from Olduvai. In the following account of the Olduvai species we have received much assistance from J. W. Simons.

Syncerus acoelotus sp. nov.

DIAGNOSIS. A *Syncerus* in which the horn cores emerge transversely, curve gradually backwards with a slight twist which is anticlockwise on the right side, but do not pass very markedly or at all ventrally in their basal parts, are internally hollowed only near their bases and as an extension of the hollowing of the frontals, are triangular in cross-section with an anterior, upper and lower surfaces, and with almost a keeled edge between the upper and anterior surfaces, and are only slightly compressed dorsoventrally. Frontals with a rugose surface in some individuals but horn cores lacking large basal bosses; anterior tuberosities of the basioccipital probably wider apart than in *S. caffer*; P_4s with paraconid and metaconid not fused but growing closer to one another.

Holotype. A cranium with both horn cores 068/5811 recovered in 1962 (Pl. 2). It is at present in the National Museum of Kenya, Nairobi.

Horizon. The holotype came from basal gravels at Kar K, upper Bed II, Olduvai. Some other specimens with horn cores range from middle Bed II to undivided III–IV, and teeth occur from Beds I to IV.

Remarks. The specific name refers to the absence of internal sinuses above the base of the horn cores, and is taken from the Greek κοῖλος (coelos), 'hollowed'. In the holotype the lateral parts of the occipital surface are missing, the right orbital rim is imperfect and only the dorsal surface of the left is preserved. The surface of the frontals is somewhat rugose between the horn core bases, and the frontals are only a little updomed, insufficiently so for there to be an associated concavity of the nasion. The cross-section of the horn cores is subtriangular becoming more oval towards the tips. The anterior surface of the horn cores is flattened proximally but becomes gradually more convex nearer the tips. Distally the horn cores curve very slightly downwards. From the massiveness of the horn cores and the rugosity of the frontals, the holotype seems to be a male. An atlas and axis vertebrae and probably also a third cervical are associated with this cranium.

Other crania of *Syncerus acoelotus* are now in Dar es Salaam. OF 67.48 was collected from FK West upper Bed II in 1962. It is probably a male although the horn cores are less massive at their bases and longer than in the holotype. The right horn core is complete to the tip and the partly reconstructed left is almost entire. The horn cores tend to have a flat top surface and an anterior keel in their lower parts; their basal cross-section approaches a triangular shape more than in the holotype. They emerge transversely, then curve backwards and slightly upwards, the backward component of the curvature being accentuated towards the tips. The right horn core is internally hollowed at about 120 mm above the base, but only in its posterodorsal part; there are no sinuses at about 250 mm short of the tips on either side. The frontals have a smooth top surface and extensive sinuses. They are slightly more convex longitudinally than in the holotype. The occipital surface is definitely wide, but less extremely so than in *Pelorovis antiquus*. The auditory bulla appears to have been somewhat compressed.

OF 68.274 is a juvenile collected from the surface of site Bos K III–IV in 1962. It is a skull with horn core bases and tooth rows, but without the back or base of the braincase. The horn core bases show no signs of keels; they have a more oval cross-section and are inserted with a more backward component than in adults. The right supraorbital foramen alone is preserved, and it is slightly larger than in adults. At the back of the palate the median indentation does not reach quite as far anteriorly as the two lateral ones. The vomer is almost certainly not fused with the back of the palate. Part of the left horn core of this specimen is detached from the skull and is numbered OF 68.205.

OF 68.196 collected in 1961 at VFK high in Bed III–IV, and almost certainly of Bed IV age, is labelled 'XDK IV'. It is poorly mineralized and consists of frontals with horn core bases. The occipital and ventral surface of the skull are completely absent. The frontals are flat and lack any surface rugosity, and the horn cores are hollowed as far as preserved. The horn core bases are more pear-shaped, with an approach to a posterior keel, and less triangular in cross-section than in other specimens. There is no clear anterodorsal keel. Possibly this specimen is from a female.

A much weathered frontlet of a small *S. acoelotus* was found in 1973 in Elephant Korongo in conglomerate 1·5 m above the Lemuta Member (Pl. 4, fig. 2). The horn cores are shorter and squatter than in previous examples. There is some dorsoventral compression of the horn cores, a more or less flat dorsal surface proximally, an anterodorsal keel proximally, and a slight

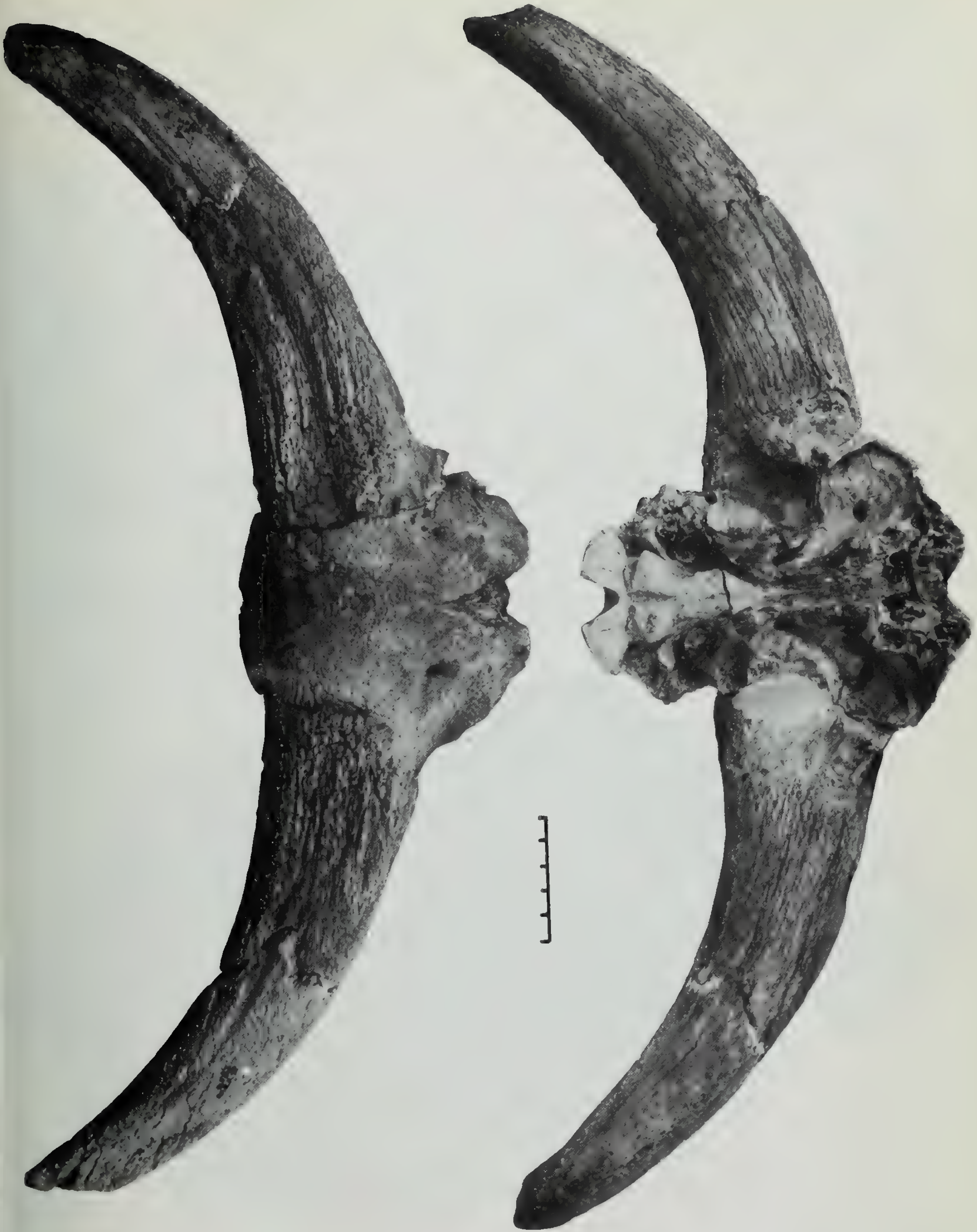

Plate 2 (Scale = 100 mm)

Syncerus acoelotus holotype. Dorsal and ventral views of cranium with horn cores, Kar K II 1962.068/5811.

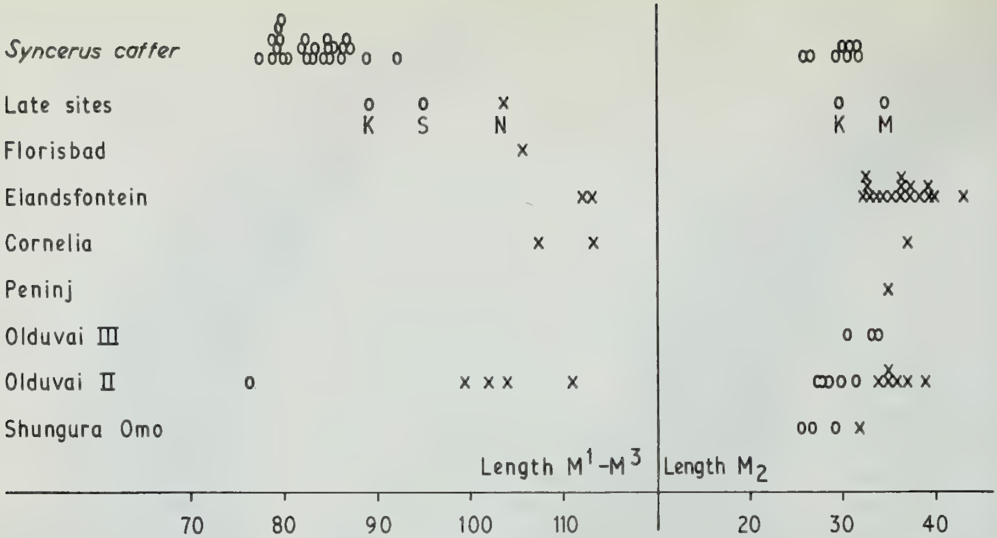

Fig. 8 Tooth measurements in Bovini. O = *Syncerus* lineage, X = *Pelorovis* lineage. K = Kibish Formation buffalo, N = Naivasha *P. antiquus*, M = Melkbos buffalo, S = '*Homoioceras*' *singae* holotype.

demarcation of a ventral and an anteroventral surface, the former being largely constituted by a posteroventral shallow concavity in the basal half of the horn core. The horn cores arise immediately behind the orbits with very wide divergence and pass slightly upwards with a gentle backward curvature. The frontals are updomed by reference to the parietal surface posteriorly, but not nearly so much as in living *S. caffer caffer*. They have a rugose surface between the horn core bases as in the holotype, and an internal system of sinuses. The top of the braincase is not very angled on the face axis, and the right temporal ridge is preserved and is as sharply demarcated as in the holotype. The chief interest of this specimen is whether the short horn cores were typical of the whole species at this early time, or whether they indicate only a forest or woodland race, comparable with *S. c. nanus* at the present day.

Bovine teeth found in Bed III, principally at the JK2 sites, seem more likely to belong to *S. acoelotus* than to *Pelorovis antiquus*, as has been mentioned already (p. 313). In Bed II some of the bovine teeth found at BK II differ from *P. oldowayensis* by being smaller (Fig. 8) and often with a more complicated occlusal morphology. They too must be *S. acoelotus*, although smaller than the Bed III teeth. In the three P_4s on BK mandibles 1953.067/5230 (Fig. 9; Pl. 1, fig. 4), 1963.2717 and 1963.2765 there is no fusion of paraconid with metaconid to form a complete medial wall at the front of the tooth, and this differs from living *S. caffer* and from *P. oldowayensis*. However, the metaconid is growing towards the paraconid, and perhaps fusion would have taken place in later wear. In the mandible 1953.067/5230 the ratio of premolar to molar row length

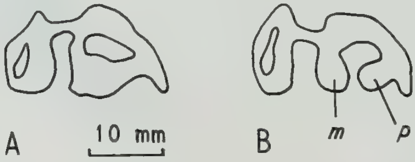

Fig. 9 Occlusal pattern of bovine left P_4s. The anterior side is towards the right of the page. A = extant *Syncerus caffer*, B = *S. acoelotus* BK II 1953.067/5230. *m* = metaconid, *p* = paraconid.

would have been greater than in most *S. caffer*, but not beyond the range for that species. A right maxilla, Rhino K 068/6655 (Pl. 3) probably from upper Bed II, has rather a large M^2 but the occlusal morphology matches *S. acoelotus*. Part of a right mandible 068/5795 may have been associated with the cranium from FK West II.

Similar bovine teeth occur at sites DK I, FLK I, FLKN I, HWK East II levels 1 and 2, and TK II. At FLKN I the teeth are perhaps less advanced than those of Bed II in occlusal complexity. It is likely that all these teeth come from a single *Syncerus* lineage, but we do not know how far back it may be called *Syncerus acoelotus*.

The fragment of right mandible with P_3 and P_4 said by Dietrich (1937 : 109; pl. 6, fig. 6) to be from STK II and described as *Bubalus* sp. was most probably of this lineage. Fusion of paraconid to metaconid on P_4 has not taken place.

Some limb bones from Olduvai are likely to be bovines of this lineage, and include a left humerus from FK West II. Others will be mentioned in the accounts of the sites, in Part II.

Survival of *Syncerus* into Bed IV at Olduvai is indicated by a bovine left M_3 and a left lower molar WK East IV A.1922 (3) and A.1698 (3), both found in 1970 and both too small for *Pelorovis*. The occlusal length of the M_3 is 45·3 mm. These teeth are counted in Tables 11 and 12 as *Syncerus acoelotus*.

The Olduvai fossils differ from the Asian water buffalo *Bubalus arnee* in that the front of the horn cores is closer to the back of the orbits, the triangularity of the horn core cross-section is less distinct since the anterodorsal edge between the top and the front surface of the horn cores is less marked and set at a less anterior level, the orbital rims project less, there is a tendency to an irregular bony growth over the surface of the frontals between the horn core bases which seems to foreshadow boss formation, and the supraorbital pits are set closer together. The distance between the supraorbital pits expressed as a percentage of skull width across the back of the orbits was 49 in the holotype of *Syncerus acoelotus*, whereas in eight skulls of *B. arnee* it had a range of 55–62, with a mean value of 58 (Gentry 1967 : 271). These characters all take the fossils closer to

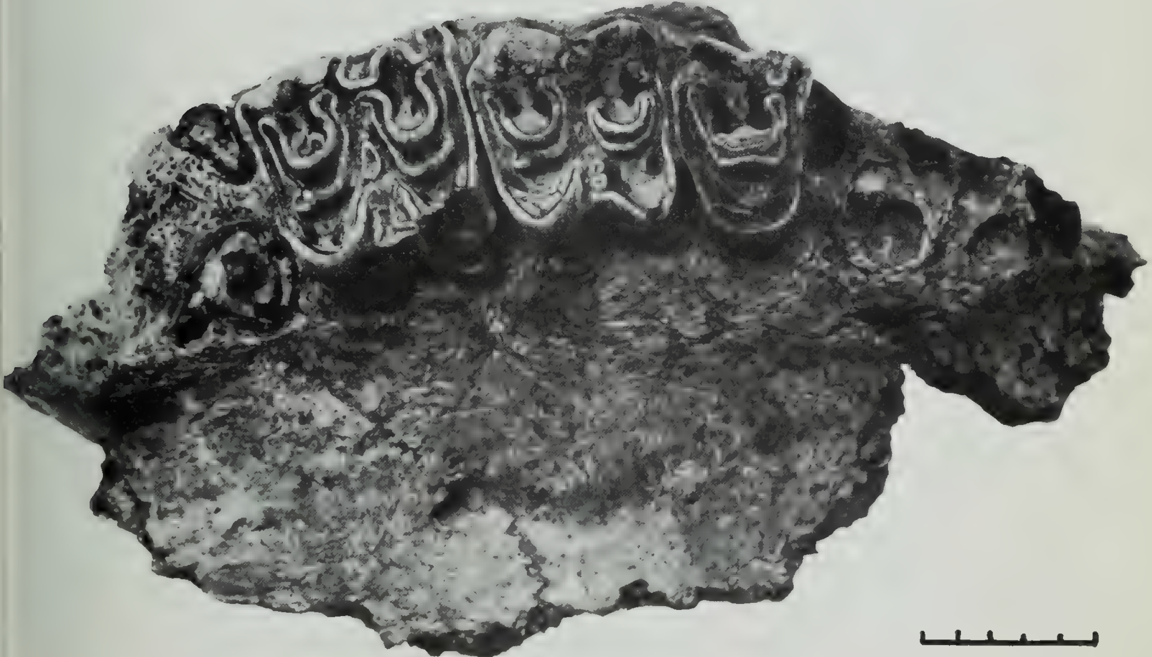

Plate 3 (Scale = 25 mm)

***Syncerus acoelotus*.** Right maxilla with P^4–M^2, Rhino K II surface 1962.068/6655.

Syncerus caffer, and we can be sure that *S. acoelotus* does not represent an Asian element in the Olduvai fauna. On the contrary, it appears to be very close to the living African buffalo.

Grubb (1972) accepts a minimum of four subspecies within the living *Syncerus caffer*. *S. c. nanus* comprises small forest forms with short horns inserted widely apart, curving outwards and backwards from the base, and lying more or less in the facial plane. There is frequently an anterodorsal keel on the horn cores between the dorsal surface and what almost amounts to an anterior surface. *S. c. brachyceros* embraces the west African savannah buffaloes ranging as far east as the River Chari. They intergrade clinally along their boundary with *S. c. nanus*, and are larger, the males having more divergent horns, dipping slightly from the facial plane and with bases approaching closer to the midline of the skull. *S. c. aequinoctialis* intergrades secondarily with *S. c. brachyceros* in the Chari region and ranges further east into the Sudan. It is a still larger savannah buffalo with larger horns which dip ventrally. *S. c. caffer* embraces the eastern and southern savannah or Cape buffaloes. The males are characterized by greatly enlarged horn bases approaching very closely to one another across the top of the swollen frontals, and horn cores dipping considerably downwards and showing so much dorsoventral compression that hardly anything of an anterior surface remains at all. Buffaloes of either of the last two subspecies intergrade secondarily with forest buffaloes along the western or Albertine Rift Valley.

There is no doubt that the Olduvai buffalo agrees most nearly with buffaloes of the first two subspecies despite their smaller size. If a forest buffalo were to grow larger without acquiring the horn specializations of the Cape buffalo, it would much resemble *S. acoelotus*. Valid differences of *S. acoelotus* from *S. caffer* remain as the less extensive hollowing of the horn cores, less dorsoventral flattening of the horn core, less complete fusion of paraconid with metaconid on P_4 and wider anterior tuberosities of the basioccipital. One can see it as ancestral to *S. caffer*, and the present-day Cape buffaloes as a very late specialization in which the great growth of the basal bosses is linked with downturning and dorsoventral flattening. Perhaps we are witnessing the origin of a new species for which the evolutionary opportunity may have been the recent disappearance of *Pelorovis antiquus*.

MEASUREMENTS. Measurements on the cranium 068/5811 from Kar II are:

Length of horn core along its front edge	*c.* 650·0
Anteroposterior diameter of horn core at its base	137·0
Mediolateral diameter of horn core at its base	110·0
Minimum width across lateral surfaces of horn core pedicels	256·0
Width across lateral edges of supraorbital pits	125·0
Occipital height from top of foramen magnum to top of occipital crest	76·0
Width across posterior tuberosities of basioccipital	72·6

Measurements on the cranium OF 67.48 from FK West II are:

Length of left horn core along anterodorsal keel	680·0
Length of right horn core along anterodorsal keel	800·0
Occipital height from top of foramen magnum to top of occipital crest	77·5
Width across posterior tuberosities of basioccipital	72·8

Measurements on the cranium OF 68.196 from VFK III–IV are:

Anteroposterior diameter of horn core at its base	*c.* 109·0
Mediolateral diameter of horn core at its base	*c.* 73·0
Width across lateral edges of supraorbital pits	135·0

Measurements on the immature cranium OF 68/274 from the surface of Bos K III–IV are:

Occlusal length deciduous P^2 to deciduous P^4	*c.* 68·0
Occlusal length M^2	*c.* 32·0

Measurements on the frontlet S.271 from Elephant Korongo, middle Bed II are:

Length of horn core along its front edge	370·0
Anteroposterior diameter of horn core at its base	103·0
Mediolateral diameter of horn core at its base	82·6

The maxilla BK II 1963.2757 had occlusal lengths M^1–M^3 and M^2 of 76·3 and 27·1 mm, and the maxilla Rhino K 068/6655 had M^2 at 31·4 mm.

Measurements on mandibles likely to be *Syncerus acoelotus* are:

	BK II 1953.067/5230	BK II 1963.2717	BK II 1963.2765	JK2 GP8 III GN 24
Occlusal length M_1–M_3	91·4	–	–	101·1
Occlusal length M_2	28·7	–	29·9	30·8
Occlusal length P_2–P_4	*c.* 56·0	56·8	*c.* 58·0	–

Occlusal lengths of M_2 on four mandibles are:

FK West II 068/5795	28·0	BK II 1963.2818	27·9
BK II 1953.067/5229	31·5	JK2 III A.2833	33·3

Measurements of length and least thickness of two limb bones of *S. acoelotus* are:

Metatarsal	SC II 1962.068/6662	228 × 31·3	Metacarpal	BK II 1952.218	217 × 38·1

COMPARISONS. *S. acoelotus* is distinguished from '*Homoioceras*' *singae* Bate of the Sudan (see p. 309) by the triangular cross-section, little dorsoventral compression, better-marked anterodorsal keel of the horn cores and wider anterior tuberosities of the basioccipital. '*H.*' *singae* can probably be regarded as a large race of *Syncerus caffer* in which the basal bosses and downward sweep of the horn cores of *S. c. caffer* are lacking. It has sinuses extending into its horn cores to at least 140 mm above the dorsal base, and probably they would have extended still further in those parts of the horn core which are not preserved.

A skull and nearly complete skeleton of a large *Syncerus caffer* were found by the 1967 Kenya contingent of the Omo Research Expedition at site KS in the same horizon of the Kibish Formation as a human skeleton (R. E. F. Leakey 1969 : 1132). The skull differs from *S. c. caffer* in the lack of any pronounced uparching of the frontals connected with basal boss formation on its horn cores, in the lack of surface rugosity of the frontals and in the horn cores not passing appreciably downwards after their emergence from the frontals. The skull resembles the less advanced west African and Ethiopian buffaloes more than *S. c. caffer*, yet it is the size of a rather large male of the latter subspecies. It differs from *S. acoelotus* in the horn cores becoming very dorsoventrally compressed immediately above the base, and in the tips being more strongly curved upwards. The limb bones are larger than half a dozen examples of living *S. c. caffer*. The metasarsals are missing, but the metacarpal may be relatively slightly longer. Morphologically the limb bones resemble *Syncerus* in the valley between the articular head and great trochanter of the femur, the short medial malleolus at the distal end of the tibia (by reference to the tibia's central anterior flange and not to the back of the medial side of the bone, which is broken), and the absence of a rim on the medial side of the proximal medial facet of the radius.

Some skull fragments from the Shungura Formation including some horn cores from member C represent a small and very short-horned *Syncerus*. The horn cores, e.g. L.744-1, L.837-2 and Omo 18 sup 1967.153, have a strong concavity on the posteroventral surface near their base, and thus resemble the Olduvai frontlet from Elephant Korongo more closely than any other *S. acoelotus*. Some surface rugosity appears on the frontals between the horn bases. Like the Olduvai *Syncerus*, they are dorsoventrally compressed, with a flat dorsal surface, emerge sideways and slightly upwards from the skull and have sinuses in their frontals. As discussed above in connection with the Elephant Korongo frontlet, the shortness of these horn cores suggests either the primitive condition for the lineage or a forest-inhabiting race. The backs of two bovine crania, L.2-26 from member B and L.607-1 from member G, are probably conspecific and have a less shortened braincase than in *S. caffer*. Their occipital surfaces are as low and wide as in Cape buffaloes and relatively lower and wider than in the smaller forest buffaloes. Bovine teeth from the Shungura Formation, very like those of Olduvai Bed I, are also likely to belong to the *Syncerus* lineage.

The *Syncerus* lineage is represented at Kanjera by the back part of a left upper molar BM(NH)

M 25715, a tooth smaller and with a more complicated occlusal pattern than *Pelorovis oldowayensis* at the same site. Other Kanjera teeth of the same species are left upper molar M 25683, right lower molar M 25697, left lower molar M 25705 and left P_4 M 25678.

Bovine teeth are found in both the later and the earlier faunas of the Kaiso Formation (Cooke & Coryndon 1970 : 201, 202; the teeth M 12595a and M 12601 assigned by them to *Hippotragus* sp. are also bovine).

A large buffalo at Melkbos (Hendey 1968 : 104) is represented by a partial cranium with horn core bases, other horn cores, dentitions and limb bones. The horn cores are internally hollowed, and the extremely marked surface rugosity of the frontals extends over the entire area between the horn core bases and the mid-dorsal line of the skull. Both these characters are advanced over the condition of *S. acoelotus*, and must align the Melkbos fossils with *S. caffer*. However, they differ from living East and southern African Cape buffaloes, *S. c. caffer*, in that the horn cores pass only outwards and do not turn downwards immediately above their bases. The whole frontal area itself is flat and not domed.

At Elandsfontein the only bovine fossils not assignable to *Pelorovis* are a right lower molar SAM 20526 and a right metacarpal 20814. Their size and proportions fit *Syncerus caffer*.

A *Syncerus* is represented by a right lower tooth row from P_4 to M_3 BM(NH) M 25304, and probably by parts of an immature right and left lower dentition M 25303, from the Chiwondo Beds at Mwenirondo, Malawi. These were recorded as hippotragine by Coryndon (1966 : 66).

Bubalus andersoni Scott (1907: 256; pl. 16, figs 4 and 4a) is a large lower jaw from the Zululand coast on which only M_2 and M_3 remain, their respective occlusal lengths being given as 32 and 45 mm. This is perhaps a large fossil *Syncerus*.

At Makapansgat Limeworks two upper molars BPI M.31 and M.32 are perhaps bovine. The occlusal complexity of these teeth is not very advanced but they are not as large as in *Pelorovis oldowayensis* as known from Bed II Olduvai and Kanjera. Their basal pillars are rather small, the styles not very pronounced, the central cavities simple in outline and the outbowings of the lateral walls between the styles not very localized or pronounced. The right mandible BPI M.15 and immature left mandible M.10 referred to 'cf. *Syncerus caffer*' by Wells & Cooke (1956 : 11) have ribs on the lateral surface of the upper molars and medial surface of the lower molars better marked than in the above. Given that regional and temporal size variations might, and did, occur in either of the bovine lineages, it is difficult to know how to place the Makapansgat specimens. It is perhaps best to regard M.31 and M.32 as connected with *P. oldowayensis*, either as a rather small variety or as representing an earlier time level of the lineage than Bed II at Olduvai, and M.10 and M.15 as connected with *Syncerus*.

One of the most interesting bovines to be found in Africa is the holotype skull, BM(NH) M 25307, of *Ugandax gautieri* Cooke & Coryndon (1970 : 206; pls 17 and 18) from Kaiso Formation deposits of unknown age in the Kazinga Channel, Uganda. Although published as a hippotragine, the skull has many similarities to *Proamphibos* Pilgrim from the Tatrot Formation of the Siwaliks. Compared with BM(NH) M 26576, a plaster cast of the holotype skull of the type species *Proamphibos lachrymans* Pilgrim (1939 : 271; pl. 5, figs 3–6), *U. gautieri* agrees in its fairly large size, very little compression of the horn cores, the degree of divergence of the horn cores, their course, their inclination in side view, their fairly wide insertions with little projection of the orbital rims, no raising of the frontals between the horn core bases, a marked anteriorly-directed central indentation of the parietofrontal suture, strong temporal ridges, the degree of bending down of the braincase on the facial axis, the short braincase, small supraorbital pits, strong nuchal crests and the triangular shape of the basioccipital. The horn core on the *U. gautieri* skull does not have the strong anterior keel nor the posterolateral keel of *P. lachrymans*, but its cross-section shows the same basic shape (Fig. 10).

Ugandax gautieri has some differences from the Indian species. These are its shorter horn cores, the less orderly surface pattern of ridges and grooves at the horn core base, the insertions less far behind the orbits, lack of a preorbital fossa, a wider and less high occipital surface, the anterior tuberosities of the basioccipital further apart, a central longitudinal ridge on the basioccipital, the basisphenoid apparently rising at a less marked angle on the plane of the basioccipital, smaller basal pillars on the upper molars, and styles less pronounced and ribs less localized on the lateral walls of the upper molars. Some of these features are more primitive than in *P. lachrymans*, notably the shorter horn cores, anteroposterior level of the horn insertions, the angle of the basisphenoid, and the tooth characters, but the different surface texture at the base of the horn cores, absence of a preorbital fossa and low occipital surface suggest that *U. gautieri* is better regarded as a separate African stock which has retained some characters in a more primitive condition than *P. lachrymans*.

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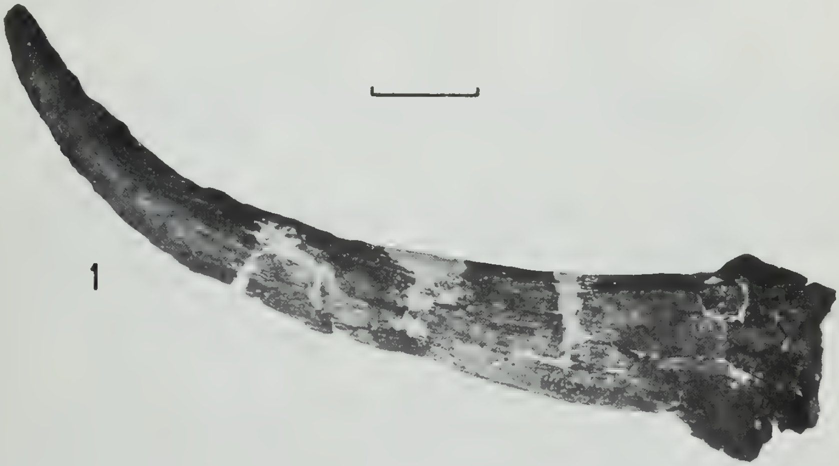

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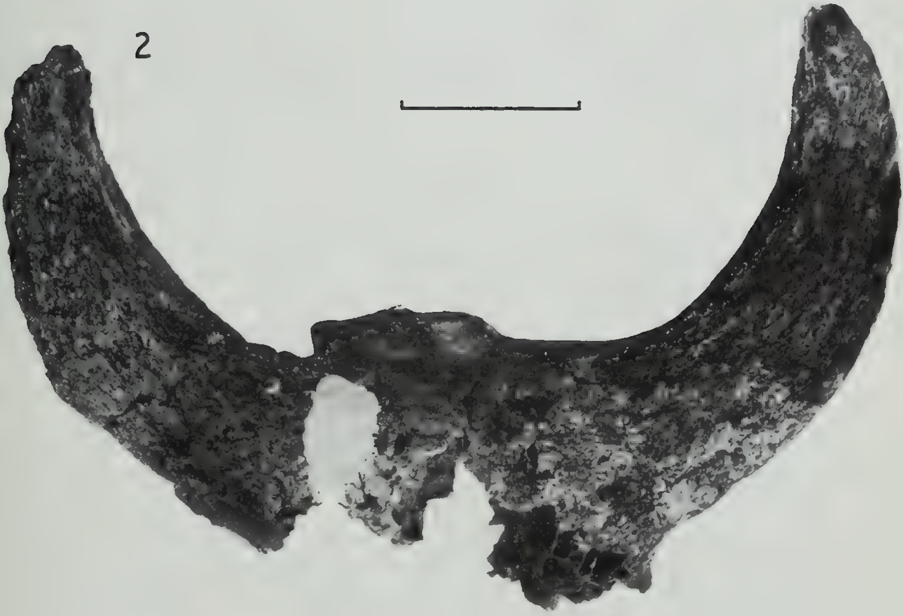


Plate 4 (Scales = 100 mm)

Fig. 1 ***Pelorovis antiquus.*** Dorsal view of right horn core, WK East IV 1970.A.2305 (5).

Fig. 2 ***Syncerus acoelotus.*** Dorsal view of frontlet, Elephant K II above the Lemuta Member.

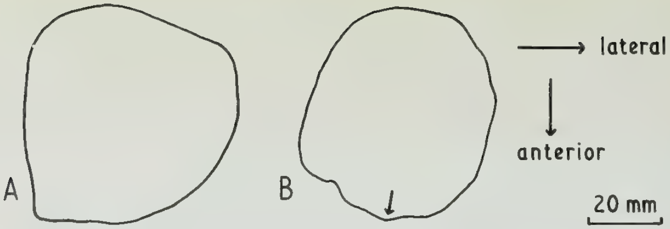


Fig. 10 Cross-sections near base of horn cores.
A = *Proamphibos lachrymans*, cast of holotype; a cross-section of the right horn core has been reversed to appear as of the left side. B = *Ugandax gautieri* holotype, left horn core. The most important of the irregular partial keels of *U. gautieri* descends at the position marked by the arrow.

Pilgrim (1939 : 276) took the reasonable view that *Proamphibos* gave rise through *Hemibos* to the living Asiatic water buffaloes *Bubalus*. If the Kazinga Channel deposits were sufficiently old, *Ugandax gautieri* could be near the start of the lineage of the African buffalo *Syncerus*. The near-absence of keels on its horn cores, less neat surface texture at the base of the horn cores, lower occipital surface, wider basioccipital anterior tuberosities and perhaps the less advanced teeth are all compatible with this view. *U. gautieri* is too primitive a species for us to expect any more definite indications of relationship. One possible intermediate between *U. gautieri* and *Syncerus acoelotus* is the Shungura Formation *Syncerus*, already mentioned above. This has an occipital surface still lower and wider than in *U. gautieri* and probably a shorter braincase, and such a trend in development of skull proportions parallels what took place in the evolution of *Bubalus*. The *Simatherium–Pelorovis* lineage is also related to the *Syncerus* lineage, and might also have come from a form like *U. gautieri*. Perhaps the three bovine successions, *Leptobos* to *Bos*, *Proamphibos* to *Bubalus* via *Hemibos*, and *Ugandax* to *Syncerus*, all arose from a genus such as *Pachyportax* Pilgrim in the upper Miocene. In view of the past connections of Indian and African bovid faunas (Gentry 1970a : 316–317) it is interesting that *U. gautieri* agrees so well with the Siwaliks *Proamphibos*. However, a careful study of the European Pliocene fossils of *Parabos* Arambourg & Piveteau might demonstrate equally close resemblances of *Ugandax* to this European bovine.

Tribe CEPHALOPHINI

Schwarz (1937 : 25) referred a mandible and some vertebrae from Olduvai to *Philantomba monticola* subsp. This species, the living blue duiker, is the smallest of the duikers and is now usually included in *Cephalophus*. Schwarz gave no illustrations and his material was lost in the Second World War. We have excluded this species from the Olduvai list.

Tribe REDUNCINI

The tribe contains two living genera, *Redunca* H. Smith, the reedbucks, and *Kobus* A. Smith, the kob, lechwes and waterbuck. Reduncines are moderate-sized to large grazing antelopes, and as indicated by their vernacular names, are commonly found in habitats near water (Lamprey 1963 : 69, fig. 7; Hirst 1975 : 32). Their characteristic skull features are: horn cores inserted above the orbits, without keels of any length or spiralling but with transverse ridges, frequently set obliquely in side view and concave anteriorly from the base up, postcornual fossae present, females without horns. Frontals with very little development of internal sinuses, frontals not rising to a higher level between the horn core bases than the top of the orbital rims, midfrontal and parietofrontal sutures fairly complicated, temporal ridges of the braincase roof often approaching closely to one another, living forms without preorbital fossae, ethmoidal fissures large, lateral flanges absent anteriorly on nasals, maxillary tuberosity prominent in ventral view, infraorbital foramen tending to be low and anteriorly-placed on the skull, basioccipital with large anterior tuberosities, foramina ovalia moderate to large, palatal ridges on the maxillae in front of the tooth rows coming close together. Teeth moderately hypsodont, rather small in relation to skull and mandible size, upper and lower molars with basal pillars, medial lobes of upper molars and lateral lobes of lower molars constricted, upper molars with small but protruding ribs between the styles, lower molars with goat folds, upper and lower P2s small, lower premolars with an appearance of antero-posterior compression, P_4s with a strongly projecting hypoconid and often a deep and narrow lateral valley in front of it, P_4s usually without paraconid–metaconid fusion to form a complete medial wall anteriorly.

Redunca redunca (Pallas 1777), the bohor reedbuck, occurs from Senegal eastwards to Ethiopia and as far south as Tanzania. It has short horns (except *R. redunca cottoni* in the southern Sudan) with tips recurved forwards. It lives in areas with long grass near water.

Redunca arundinum (Boddaert 1785), the southern reedbuck, is found from Tanzania southwards and has long and divergent horns, less thickened at the base than in *R. redunca*. About half the P_4s show close approach or even fusion of paraconid and metaconid.

Redunca fulvorufula (Afzelius 1815), the mountain reedbuck, has a discontinuous distribution in southern Africa, some parts of eastern Africa, and in northern Cameroun. It has short and little divergent horns, less thickened at the base than in *R. redunca*. The orbits are larger than in the other two species. It lives on rocky sloping grassland with light cover, which is an unusual habitat for a reduncine.

Kobus kob (Erxleben 1777), the kob, including *K. vardoni* (Livingstone 1857), the puku, occurs from south-western Kenya and Uganda westwards to Senegal and as far south as Botswana. The horn cores show some mediolateral compression, curve backwards at the base, and are inserted close together in anterior view and uprightly in side view. Gentry (1970a : 282) has commented that the limb bones are more cursorially adapted than in other reduncines. It favours grasslands close to water, frequently the higher parts of floodplains.

Kobus leche Gray 1850, the central African lechwe, has horn cores which are mediolaterally compressed, inserted wide apart and obliquely at the base, and curved backwards at the base. The species is markedly gregarious on the lowest-lying parts of floodplains.

Kobus ellipsiprymnus (Ogilby 1833), the waterbuck, is the largest living reduncine. It occurs from Somalia westwards to Senegal and as far south as Natal. The horn cores are little mediolaterally compressed, inserted wide apart and obliquely at the base, and are curved upwards from the base and eventually forwards. The species lives in savannah country with access to water and browses more frequently than *K. kob* or *K. leche*.

Kobus megaceros (Fitzinger 1855), the Nile or Mrs Gray's lechwe, occurs in marshy areas of reeds or tall grass around the papyrus 'sudd' swamps in the southern Sudan, and in the Gambella region of Ethiopia (Blower 1967). It has a very distinctive skull morphology. The horn cores are inserted further behind the orbits than in other reduncines, the braincase is short and angled on the facial axis, the nasals are wide and the longitudinal ridges on the basioccipital are very strong.

Among fossil reduncines *Kobus sigmoidalis* Arambourg is a likely ancestor for waterbuck and the central African lechwe. Fossil kobs are also known, but no distinct species have been named. Early *Kobus* seem likely to have had horn cores inserted obliquely and close together. The kob stock retained the oblique insertions for a time and showed less mediolateral compression of the horn cores than in *K. sigmoidalis*. By the time of Olduvai Bed III kobs had acquired more uprightly-inserted and more compressed horn cores, while the waterbuck line had developed less upright and less compressed horn cores. The skull became lower and wider in the latter group, rather as in *Redunca*. The living kob has acquired or retained a braincase more angled on the facial axis than in *Redunca* or other *Kobus*; it also has a noticeably smoothly-rounded edge of the occipital surface which is like some *Redunca*. Two or more reduncines from the Pinjor and Tatrot Formations of the Siwaliks are congeneric or close parallels to *Kobus*.

Redunca probably derived from smaller forms with wider skulls and more upright horn cores than *Kobus*. The only undoubted fossil species is *R. darti* Wells & Cooke. *R. ancystrocera* Arambourg may be linked with the very large and unique Olduvai fossil named *Thaleroceros radiciformis*, and is better classified as belonging to *Kobus*. A final group of reduncines, unrepresented at Olduvai, is constituted by the Omo, Kaiso and Marsabit Road (2°30′ N, 37°27′ E) form *Menelikia lyrocera* Arambourg 1941.

Genus ***KOBUS*** A. Smith 1840

TYPE SPECIES. *Kobus ellipsiprymnus* (Ogilby 1833).

GENERIC DIAGNOSIS. Larger-sized reduncines; horn cores usually long, their bases sometimes curving backwards instead of being concave anteriorly, with a flattened lateral surface but no tendency towards a flattened posteromedial surface; frontals sometimes with a small system of internal sinuses.

REMARKS. Generic level definitions are difficult and unsatisfactory in the Reduncini because of the differences within *Kobus* between kobs and the waterbuck–central African lechwe group, the uncertain generic placing of some fossils, the independent appearance of characters in different lineages, and because of some instances of opposing directions of character evolution in different lineages. Living *Kobus* species are more gregarious than reedbucks, but a behavioural trait is not useful for the interpretation of fossils.

Kobus sigmoidalis Arambourg 1941

1941 *Kobus sigmoidalis* Arambourg: 346, fig. 5.
1947 *Kobus sigmoidalis* Arambourg: 411; pl. 27, fig. 4; pl. 28, fig. 3.
1947 *Kobus* (*Kobus*) sp. Arambourg: 415, text-fig. 61.

DIAGNOSIS. An extinct species of *Kobus* about the size of the living waterbuck or central African lechwe; horn cores long, mediolaterally compressed, without keels, with transverse ridges, more divergent basally than in waterbuck then with lessening divergence distally, and with a weakly sigmoid curvature at the base so that they curve first backwards then upwards. Temporal ridges approaching quite closely posteriorly, top edge of occipital fairly evenly rounded, median occipital ridge with a flanking fairly flat surface, mastoids often with a strong ventral rim and often without a marked depression around the mastoid foramen, basioccipital with large anterior tuberosities, auditory bullae inflated and moderate-sized. Upper molars retaining the primitive characters of central cavities that are often not very complicated and ribs between the styles that are not very localized or accentuated; lower molars probably with less constricted lateral lobes more frequently than in the living waterbuck.

HOLOTYPE. A cranium, 145, found in the Omo beds in 1932–33 and now in Paris.

HORIZON. The horizon of the holotype is unknown. In the Shungura Formation the species is present in members C and D and common in E, F and G. At Olduvai it is quite common in Bed I; it occurs at Kaiso and it, or a descendant, at Kanjera.

REMARKS. *Kobus sigmoidalis* is best known from Omo. The Olduvai material is larger and includes an incomplete right horn core (Pl. 5, figs 1, 2), part of the same skull with basioccipital and auditory bullae, and nearly complete maxillae, all numbered FLKNN I 1961.871. The right side of a crushed, immature skull with horn core base 296 also came from FLKNN I. A frontlet with the basal halves of both horn cores 068/6506, and associated palate 068/6502, was found in 1961 in gravel postdating the Ndutu Beds and probably of Holocene age near the base of the Gorge at FLKNN I; from the type of fossilization and the adherent calcareous incrustation it probably originated in Bed I or lower II and was redeposited (M. D. Leakey, personal communication). The basal part of a left horn core BM(NH) M 14542 found in 1932 and the basal part of a right horn core with the midfrontal suture and supraorbital pit M 29419 both came from Bed I.

K. sigmoidalis is too large to be connected with living *Redunca* and is unlike a kob or Nile lechwe, so it is necessary to differentiate it from the waterbuck and central African lechwe. The

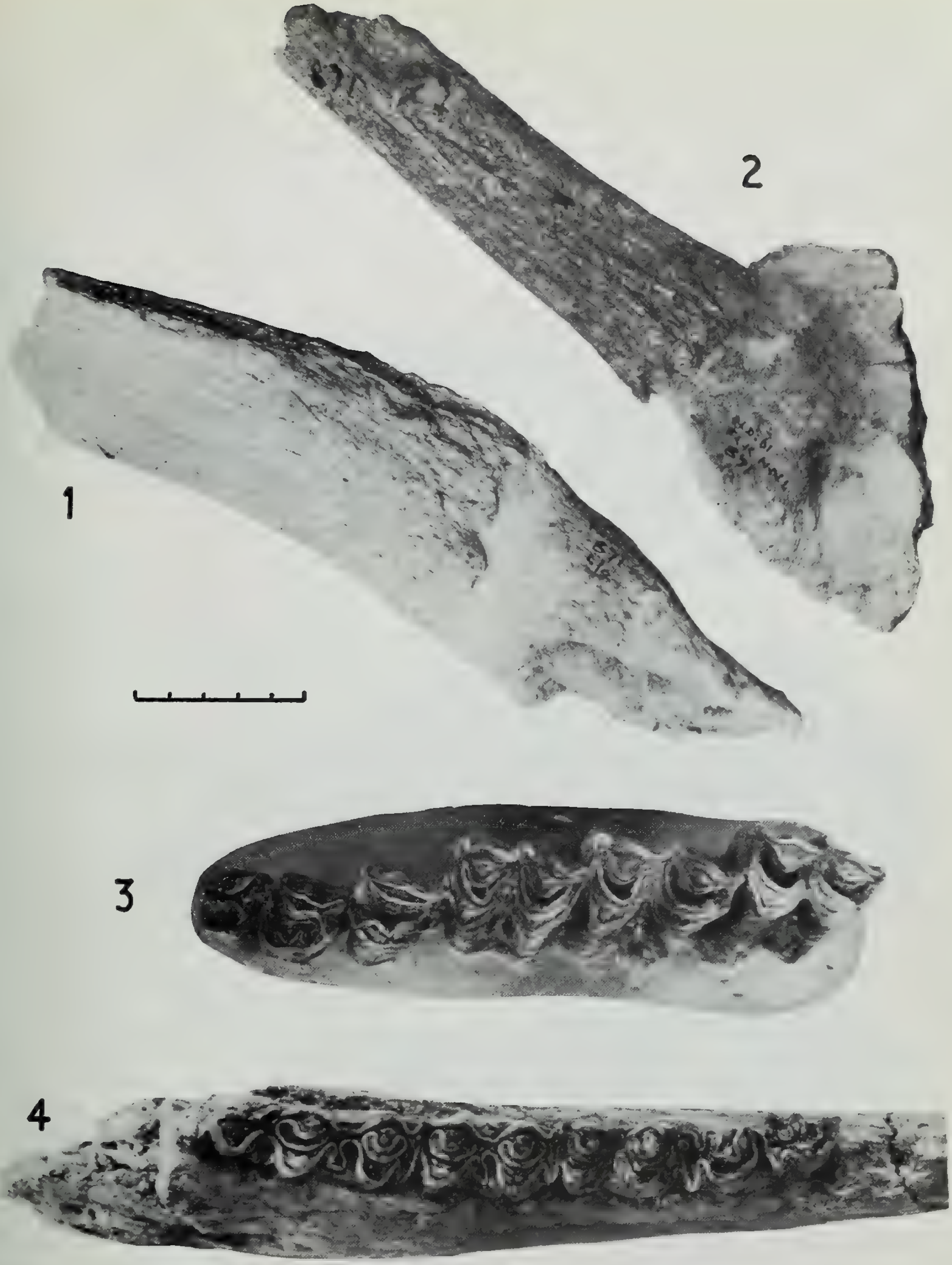


Plate 5 (Scale = 50 mm for the horn core and 25 mm for the dentitions)

Kobus sigmoidalis

Fig. 1 Lateral view of right horn core, FLKNN I 871.

Fig. 2 Anterior view of same horn core.

Fig. 3 Occlusal view of left P^2–M^3, FLKNN I 535.

Fig. 4 Occlusal view of right P_3–M_3, FLK I G.388.

differences from the waterbuck comprise the characters mentioned in the diagnosis with the reservation that not all available individuals of the living species, or even a majority of them, have more advanced upper molars. The living waterbuck is larger, its horn cores are less compressed (Fig. 11), less divergent and often shorter, beginning to rise from their bases instead of from their middle sections, the temporal ridges are wider apart, the occipital surface has pronounced hollows on either side of its median vertical ridge and its edge is not smoothly rounded, the mastoids are larger, without a pronounced ventral rim and frequently with a small deep depression around the mastoid foramen.

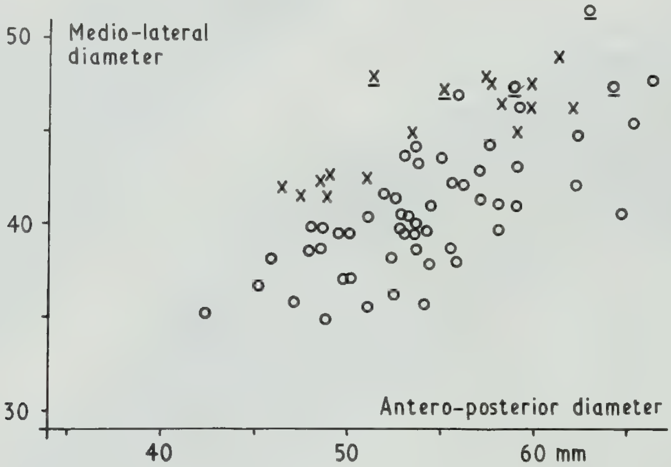


Fig. 11 Basal horn core dimensions of some reduncines.

O = *Kobus sigmoidalis* from member G of the Shungura Formation, X = *K. ellipsiprymnus*, O̲ = Olduvai *K. sigmoidalis*, X̲ = Olduvai *K. ellipsiprymnus*. *K. sigmoidalis* is larger at Olduvai than at Omo.

In all these characters *K. sigmoidalis* resembles the lechwe *K. leche*, but we prefer to regard it as no more closely related to this species than to *K. ellipsiprymnus*. Our opinion arises from the teeth of Olduvai *K. sigmoidalis* being much larger than those of *K. leche* and from the horn core evidence of a transition from *K. sigmoidalis* to *K. ellipsiprymnus*. Good *K. sigmoidalis* occurs as high as member G of the Shungura Formation and early in Olduvai Bed I. A minority of Shungura member G horn cores, e.g. L.25-15 and L.518-8, are intermediate between *K. sigmoidalis* and *ellipsiprymnus* in the degree of basal backward curvature and mediolateral compression. Probably the transition to *K. ellipsiprymnus* occurred within the time span of Olduvai. Horn cores from Beds I?, III and the III–IV junction, and some Shungura pieces, e.g. F.203-27 from member K and the middle part of a horn core F.164-25 from member G, are more definitely like waterbuck. *K. leche* is perhaps also a descendant of *K. sigmoidalis*, showing less alteration in its morphology but a specialized way of life.

A hornless female skull of a large *Kobus* S.202 (Pl. 6) was found in Bed I in 1970. It came from geologic locality 63. It is almost complete and lacks only the left P^4, right premaxilla, top of the left premaxilla, front of the nasals and part of the zygomatic arch. Some distortion has occurred. It is smaller than adult females of the living waterbuck, the back half of the braincase probably descends rather steeply, and the basioccipital has a markedly deep central longitudinal groove. The identification of this specimen as *K. sigmoidalis* or *ellipsiprymnus* is difficult: the temporal ridges approach one another closely, the mastoid is slightly narrower than in the waterbuck and lacks a pronounced ventral rim, and the median occipital ridge and flanking hollows are slightly better marked than in some Omo male *K. sigmoidalis*. We will take this suite of characters as supporting assignment to *K. sigmoidalis*, but it does not seem very decisive particularly if one reflects that early *K. ellipsiprymnus* would not be so distinct from *K. sigmoidalis* as is present-day *ellipsiprymnus*.

The considerable number of reduncine dentitions from Olduvai Bed I, including many immature ones, agree in size and morphology with those associated with the horn core 871 and frontlet 068/6506, and on the female skull S.202. They are presumably all of *K. sigmoidalis* or perhaps early *K. ellipsiprymnus*. The adult tooth rows are about the size of those of living waterbuck, but

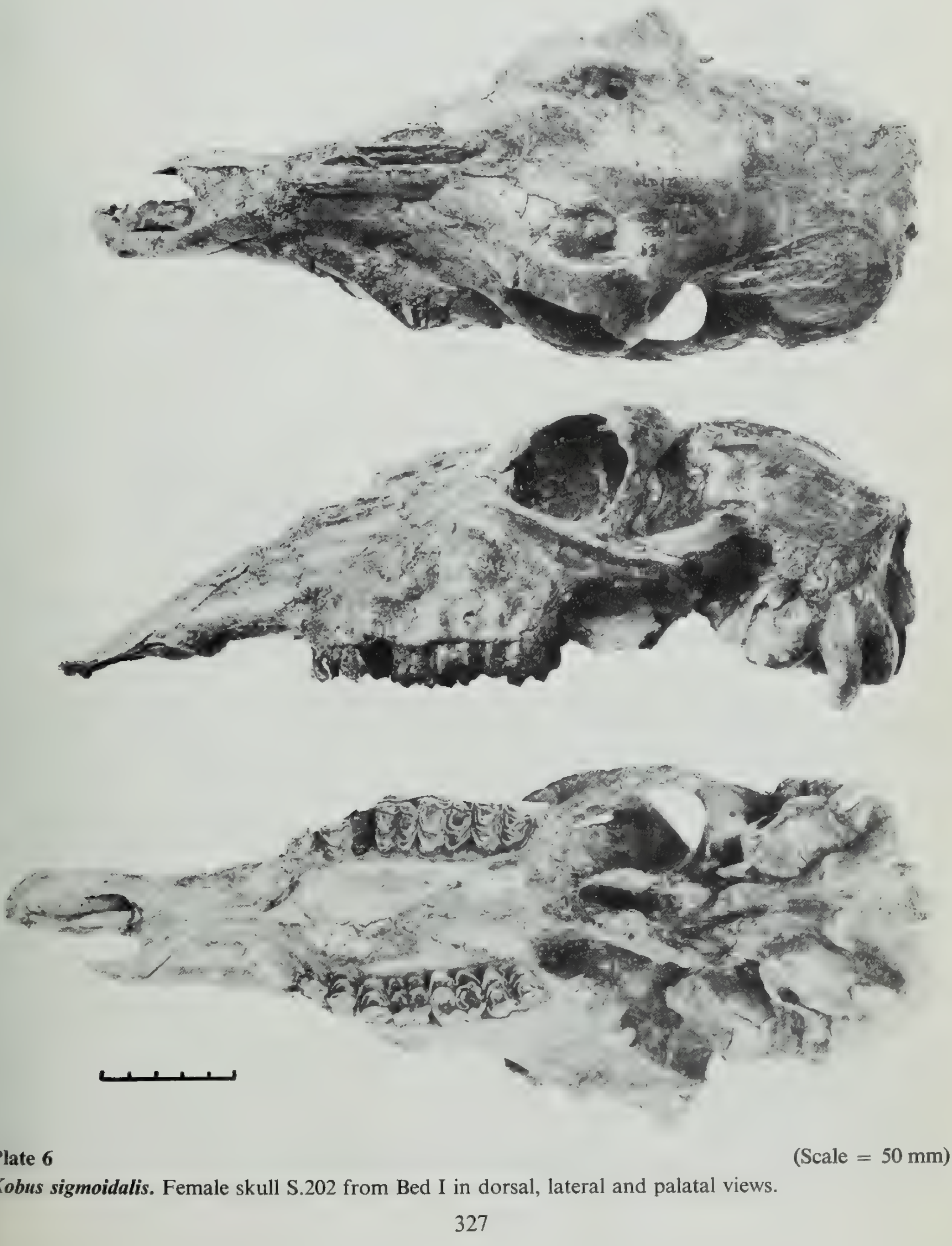


Plate 6 (Scale = 50 mm)

Kobus sigmoidalis. Female skull S.202 from Bed I in dorsal, lateral and palatal views.

four measurable specimens (maxilla FLKNN I 535, skull S.202 and mandibles FLKNN I 64 and FLK I D.41) suggest that the premolar row could be shorter. Both mandibles have premolar row lengths at the lower end of the distribution for Recent *K. ellipsiprymnus* (Fig. 12). As already mentioned, *K. sigmoidalis* molars have a rather unprogressive morphology, and this is true of specimens in a middle stage of wear which is the period when any evolving complexity would be most easily detectable. Large samples of teeth from the living species and from successive horizons at Olduvai and other sites could be expected to demonstrate the gradual appearance of, for example, localized and accentuated ribs on the lateral walls of the upper molars. Reduncine teeth of a size appropriate for *K. sigmoidalis/ellipsiprymnus* continue to occur in lower Bed II, and there is a single occurrence from middle Bed II just above the Lemuta Tuff Member. This is a left M_3 HWK EE II 1123 with an occlusal length of 30·2 mm.

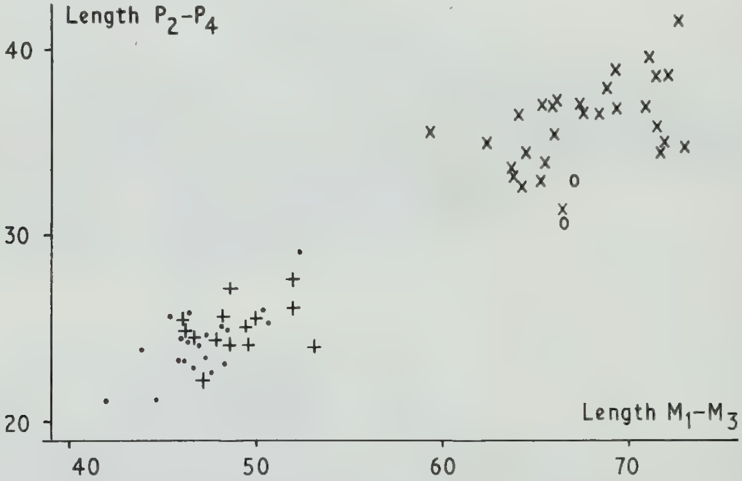


Fig. 12 Premolar/molar row proportions for some reduncines.
X = living *Kobus ellipsiprymnus*, + = living *K. leche*, ● = living *K. kob*, O = right mandibles FLK I 1960.D41 (above) and FLKNN I 1960.64 (below).

The Bed I reduncine limb bones are also probably of *K. sigmoidalis*. Fig. 13 (p. 332) shows that the long metapodials and rather long radius have proportions nearer to lechwe than to waterbuck. Further details are given in the account of the FLKNN I site in Part II.

MEASUREMENTS. Measurements on *K. sigmoidalis* are:

	FLKNN I 871	FLKNN I 068/6506 +068/6502	Bed I M 29419
Anteroposterior diameter of horn core at its base	64·3	59·0	63·1
Mediolateral diameter of horn core at its base	47·6	47·3	51·5
Occlusal length M^1–M^3	–	67·8	–
Occlusal length M^2	21·0	c. 23·7	–

Measurements on the female skull S.202 are:

Skull length from front of the premaxillae to back of the occipital condyles	332·0
Skull width across posterior side of orbits	131·0
Width across lateral edges of supraorbital pits	67·6
Length from back of frontals to top of occiput	77·8
Maximum braincase width	84·9
Skull width across mastoids immediately behind external auditory meati	100·5
Distance from rearmost point of occlusal surface of M^3 to back of occipital condyles	140·0

Occipital height from top of foramen magnum to top of occipital crest	45·4
Occlusal length M^1–M^3	57·1
Occlusal length M^2	19·6
Occlusal length P^2–P^4	34·2

Measurements on two maxillae assigned to *K. sigmoidalis* are:

	FLKNN I 535	FLK I B.46
Occlusal length M^1–M^3	63·1	–
Occlusal length M^2	22·8	21·5
Occlusal length P^2–P^4	40·2	–

Measurements on the more complete mandibles assigned to *K. sigmoidalis* are:

	FLKNN I					FLK I	
	13	64	131	920	965	D.41	G.388
Occlusal length M_1–M_3	–	66·6	–	63·5	77·8	67·1	68·0
Occlusal length M_2	–	20·2	20·1	20·4	23·2	20·8	20·2
Occlusal length P_2–P_4	35·1	30·7	35·2	–	–	33·0	–

Measurements on the M_2s of 10 mandibles from FLKNN I and FLK I, including those from the mandibles whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_2	10	21·1	20·1–23·2	1·1	0·35

Measurements of length and least thickness on some associated sets of limb bones assigned to *K. sigmoidalis* are:

FLKNN I	radius 370	244 × 34·2,	metacarpal 369	230 × 28·0
FLKNN I	radius 890	250 × 29·2,	metacarpal 889	228 × 24·1
FLKNN I	radius 499	249 × 37·5,	metacarpal 498	238 × 28·7
FLK I	radius C.1094	259 × –,	metacarpal C.1095	241 × –
	humerus C.1092	270 × 31·7		

Measurements of length and least thickness of other limb bones assigned to *K. sigmoidalis* are:

DK I	radius 788	236 × 34·5
FLKNN I	metacarpal 616	205 × 20·3
FLKNN I	metatarsal 738	225 × 25·3

COMPARISONS. The base of a right horn core from Kanjera, BM(NH) M 25633, is either *K. sigmoidalis* or *K. ellipsiprymnus* on account of its degree of mediolateral compression and absence of backwardly-directed curvature at the base.

An unregistered left horn core in London, labelled 'KAISO I', much resembles *K. sigmoidalis*. This may be the piece collected by Bishop at Nyawiega which Cooke & Coryndon (1970 : 214) referred to *Pultiphagonides* cf. *africanus*. It is interesting that Nyawiega fossils are thought to come from the earlier Kaiso faunal assemblage, perhaps as old as 4–5 million years, which would make the Nyawiega horn core older than the *K. sigmoidalis* of the Shungura Formation, Omo.

A cranium L.2604 and some short horn cores from Langebaanweg may be a *Kobus* species (Gentry *in* Hendey 1970a : 115). The oblique horn core insertions and very upright pedicels, and the closeness of the insertions, could all be primitive in *Kobus*. A flattened lateral surface and some degree of mediolateral compression are like *K. sigmoidalis*. The species is unlikely to belong to *Redunca* since it is larger than the Makapansgat Limeworks fossil *R. darti*, has more oblique and closely inserted horn cores, a higher occipital surface without an evenly rounded edge, large auditory bullae, larger anterior tuberosities of the basioccipital and larger mastoids without a ventral rim. The best solution seems that the Langebaanweg remains represent a short-horned relative or ancestor of *K. sigmoidalis*.

One of the reduncine crania from the Pinjor Formation of the Siwaliks and now in London has some resemblance to *Kobus sigmoidalis*. This is BM(NH) 39559a, referred to as *Vishnucobus patulicornis* (Lydekker) by Pilgrim (1939 : 102). It is a little smaller than *Kobus sigmoidalis*, and agrees in having fairly divergent horn cores. It is unlike the East African species in its larger supraorbital pits situated close together, and more primitive in its prominent temporal ridges and less compressed horn cores inserted more closely together. If the Pinjor Formation were earlier than the later levels of the Shungura Formation at Omo, it is possible that 39559a might be the actual ancestor of *K. sigmoidalis*. Further discussion of Siwaliks reduncines will be found under kob on p. 337.

The type cranium of *Kobus venterae* Broom (1913 : 13) from Florisbad, SAM 2323, differs from *K. leche* only in the slightly more upright horn core insertion in side view, but the doubtful precision with which the horn core has been affixed makes this uncertain. The skull is low and wide and lechwe-sized. The horn cores would have been inserted wide apart in anterior view and above the back of the orbits. The surviving right horn core is very compressed with a flattened lateral surface and lacks keels or transverse ridges. It has a slightly convex front edge in profile at the base as in *K. sigmoidalis*. The upper part of the median occipital ridge is preserved and shows shallow hollows on either side. The mastoid exposure is moderately-sized. There is no clear sign of a ventral rim to the mastoid, nor of the small depressed area cut dorsomedially quite deeply into the occipital, frequently found in the waterbuck. The anterior tuberosities of the basioccipital are not as large as in the waterbuck and resemble the lechwe. The cranium is best regarded as belonging to *K. leche*. Similar horn cores in Bloemfontein from late Pleistocene sites are probably the same species. Several specimens come from Florisbad, including an unnumbered frontlet and left and right horn cores both numbered C.1458, which are larger than the holotype, two left mandibles, C.1473 and one without number, and a left lower molar. Other horn cores come from Mahemspan (C.1940), Mockesdam (C.2679), Vlakkraal (four numbered C.1541) and Cornelia (Cooke 1974 : 77). These remains give valuable information for palaeoecological analysis, because of the close association of *K. leche* with seasonally inundated flood plains.

Kobus ellipsiprymnus (Ogilby 1833)

Diagnosis. A large reduncine species; horn cores moderately long with some mediolateral compression, little or moderate divergence, transverse ridges generally well marked, without any backward curvature at the base but rising with their concave edge anteriorly; temporal ridges of the cranial roof may approach closely or remain more widely apart; top edge of occipital not evenly rounded, median ridge on the occipital flanked by small depressions near its top; mastoids not narrow, without a strong ventral rim but with a marked depression around the mastoid foramen, and tending to face laterally in males. P_4s in late wear may show fusion of paraconid and metaconid.

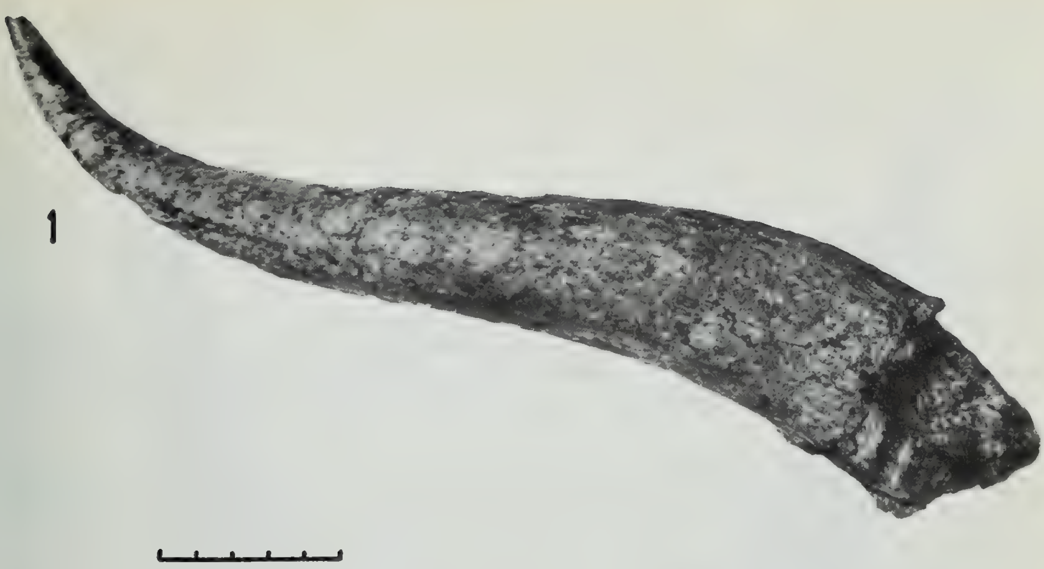
Remarks. Some Olduvai horn cores are likely to be of waterbuck, as previously mentioned in the discussion of *K. sigmoidalis*. These are a left horn core with the frontal suture, supraorbital pit and orbital rim 068/6658 from the surface of EF-HR III–IV junction in 1962 (Pl. 7, fig. 2), the basal part of a left horn core JK2 GP8 III 1654 found in 1961, the lower part of a probably left horn core BM(NH) M 14536, part of a right horn core M 14537 and perhaps the base of a right horn core with part of the frontal M 29423. The first two London specimens were found in 1932 and are supposedly from Bed I. M 29423 is of unknown horizon ('? Bed I') and was found in 1931. These horn cores are not very curved backwards at the base, not mediolaterally compressed, have a flattened lateral surface and are less divergent than in *K. sigmoidalis*.

A left lower molar JK2 III B.FFM4-9 is larger than three teeth assigned to kob from the JK2 sites and could belong to a waterbuck.

Measurements. Anteroposterior and mediolateral diameters at the base of the horn cores are:

EF-HR III–IV surface 068/6658	51·4 × 48·1
BM(NH) M 14536	55·3 × 47·3
BM(NH) M 29423	50·1 × 46·1

1



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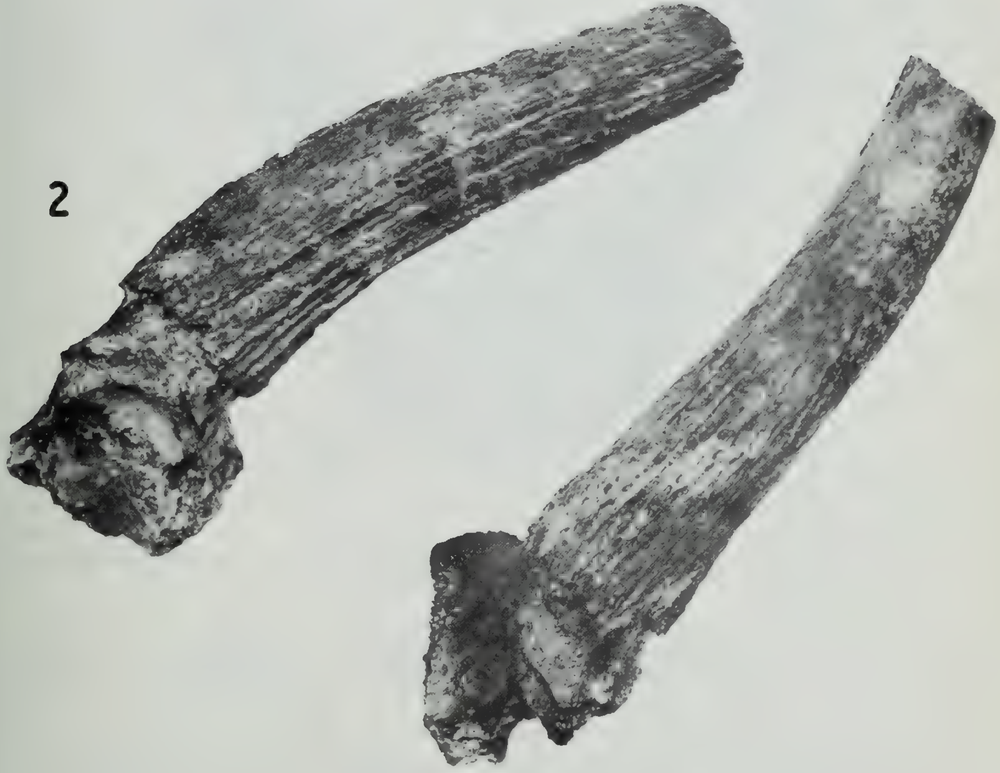


Plate 7 (Scale = 50 mm)

Fig. 1 ***Kobus kob.*** Lateral view of right horn core, JK2 GP8 III 1247.

Fig. 2 ***Kobus ellipsiprymnus.*** Lateral and anterior views of left horn core, EF-HR III–IV surface 068/6658. (Originally marked as from DK.)

COMPARISONS. A few horn cores from member K and the middle part of a horn core, F164-25 from member G, represent the waterbuck in the Shungura Formation, Omo.

A left upper molar BM(NH) M 25301, said to be of caprine type by Coryndon (1966 : 65), represents a waterbuck-sized reduncine in the Chiwondo Beds of Mwenirondo, Malawi. Its occlusal length is 21·9 mm.

Kobus kob (Erxleben 1777)

1965 *Kobus* sp. A Leakey : 47.
1965 *Kobus* sp. B Leakey : 47.

DIAGNOSIS. A species of *Kobus* smaller than waterbuck or lechwe; horn cores with some medio-lateral compression, curving backwards at the base, inserted close together and fairly uprightly; large supraorbital pits; skull not wide; braincase angled quite strongly on the facial axis; occipital surface with an evenly rounded top edge; narrow mastoids often having a strong ventral rim in males.

REMARKS. Remains of kob are not very common at Olduvai Gorge. The larger *Kobus sigmoidalis/ellipsiprymnus* lineage occurs in Bed I sites other than FLKN, but disappears in Bed II after HWK EE. Thereafter in Bed II one finds much sparser remains of kob, although both kob and waterbuck occur in Bed III. The Olduvai kob need not be separated from the living species.

The skull, dentitions and partial skeleton of a kob were excavated from MNK middle Bed II in 1963. The skull, 104 + 106, is incomplete and unfortunately rather crushed but does show the reduncine lack of a preorbital fossa. It is hornless but has the slight horn core rudiments of a reduncine female. The auditory bullae are large and inflated. The mandibles, right 107 and left 108, and right maxilla 103 are considerably smaller than those of *Kobus sigmoidalis*. The premolar rows are incomplete, only P_4 being preserved on each side, but the molar rows are the size

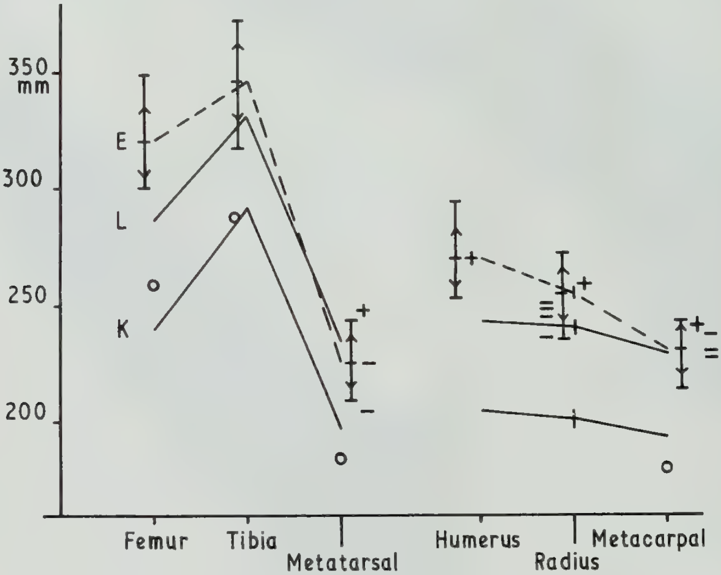


Fig. 13 Lengths of limb bones in Reduncini.

E = mean of 11 *Kobus ellipsiprymnus*, with ranges and standard deviations, L = a single *K. leche*, K = mean of 4 *K. kob*, O = the kob-sized reduncine from MNK II, + = reduncine from FLK I (humerus C 1092, radius C 1094, metacarpal C 1095).

Readings for other Bed I fossils are shown by the horizontal dashes; the relatively long metacarpals compared with the radii agree with the proportions of *K. leche* rather than *K. ellipsiprymnus*.

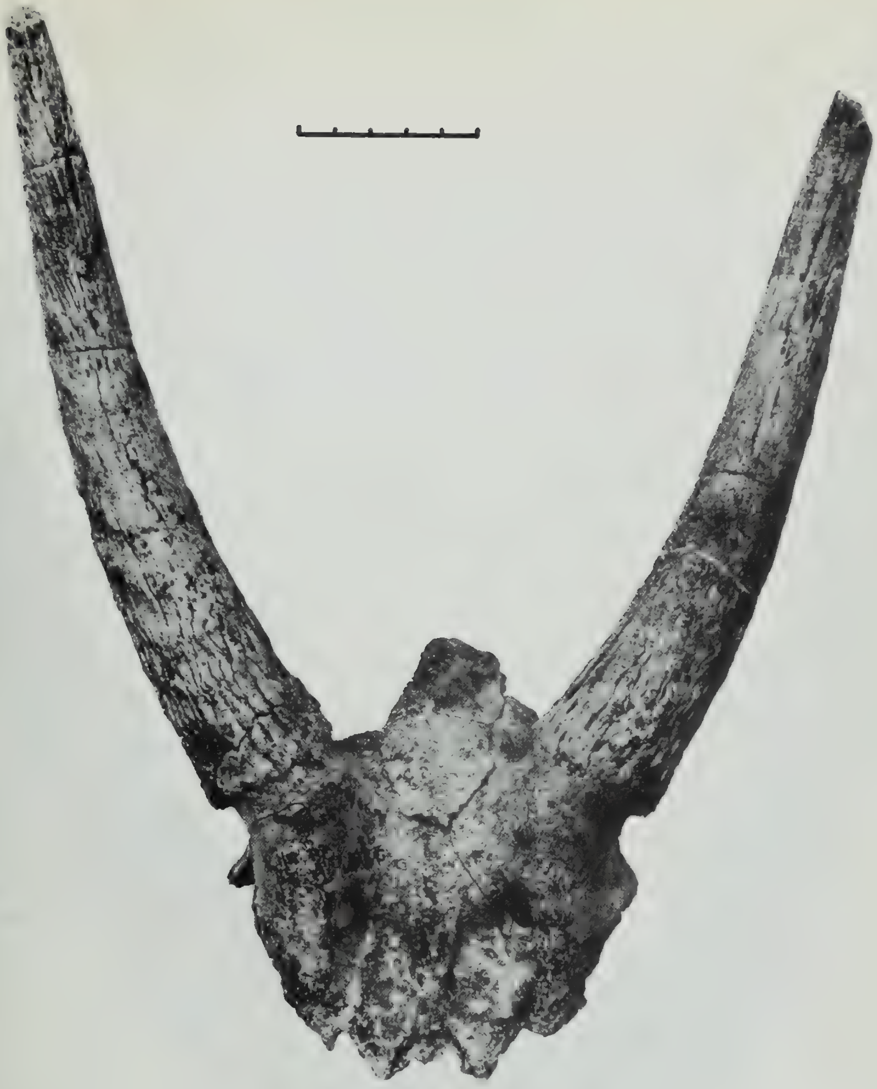


Plate 8 (Scale = 50 mm)
Kobus kob. Dorsal view of frontlet, ? MRC II 1962.068/6659.

of a lechwe or large kob. The upper teeth show less complicated central cavities and less accentuated and localized ribs between the styles than in living kob, but this difference might vanish after a little more wear. The skeleton preserved consists of the atlas vertebra 110 and a number of limb bones of the right side. These are the metacarpal 105, ulna 109, femur 101, tibia 102 and metatarsal 100. They fit a reduncine smaller than *K. sigmoidalis/ellipsiprymnus*. Identification as reduncine rather than tragelaphine is based on the slight medial tuberosity on the magnum–trapezoid facet of the metacarpal and posterolaterally a backwardly-pointed projection on the unciform facet, the fairly deep groove between the front and rear naviculocuboid facets and the poor anterior longitudinal groove on the metatarsal, and the deep hollows on the sides of the distal condyles of both the metacarpal and metatarsal. Their association with the skull and dentitions confirms this identification. Compared with four examples of living *K. kob* the femur of this individual is rather long and the metapodials rather short (Fig. 13); such proportions would not be surprising in an earlier kob.

Three Olduvai specimens give an indication of what the horn cores were like during Bed II times. These are a frontlet with complete horn cores 1962.068/6659 from upper Bed II (Pl. 8), a frontlet with incomplete horn cores P.P.R.1 from BK II East in 1953 (Leakey 1965 : 47, *Kobus* species A), and a left horn core SHK II 1957.579, a surface find (Leakey 1965 : 47, *Kobus* species B, said to be a right horn core but actually a left). 'GTC' is written on the first frontlet, which is inappropriate for its adherent Bed II matrix; however, the original inscription was MRC and this is a site near GTC at which Bed II does occur. These horn cores differ from living kob in being set quite obliquely in side view; they begin to curve upwards near the base and show less backward curvature at the base, being inserted quite widely apart and having very little mediolateral compression. The frontlet 1962.068/6659 is possibly sub-adult, and might have developed more basal backward curvature at a later age. The horn cores differ from those of *K. sigmoidalis* and *K. ellipsiprymnus* in being smaller, having less widely-set insertions and being less divergent: in addition the supraorbital pits are larger.

Two isolated reduncine teeth from Bed II are an appropriate size for the kob. These are left M_3s SHK II 1957.396 and BK II 1957.1362. A nearly complete left humerus BK II East 1953.442 and the distal end of a left humerus BK II 1957.42 are also likely to be of kob by their combination of slanted condyles with a deep hollow for the posterolateral humeroradial ligament.

The kob horn cores from Bed III differ from those of Bed II in being larger and longer, curving backwards at the base from a more upright insertion, and in having rather more mediolateral compression. They thus approach living kob more closely, but still differ in being larger, less uprightly inserted at the base and the insertions being less close together. The two specimens, both found at JK2 GP8 III in 1962, are a right horn core 1247 (Pl. 7, fig. 1) and a frontlet with complete left and nearly complete right horn core 068/6694 (Pl. 9). On the latter the backwardly curved basal part of the horn core is beginning to be a little less divergent than the middle part, which is an approach to the morphology of modern kob. These Bed III horn cores differ from those of *K. ellipsiprymnus* in being more curved back at the base, more compressed and probably less divergent, and 1247 shows quite a large internal sinus in its frontal extending into part of the pedicel. They are less divergent and have larger supraorbital pits than *K. megaceros*. They differ from *K. sigmoidalis* and *K. leche* in being less divergent and less mediolaterally compressed. An Olduvai horn core collected by Wayland in 1934, BM(NH) M 26928, is quite likely to belong here, but its horizon is unknown.

A right lower molar JK2 b III, a deciduous left P_4 JK2 III A.3271 M8, and a left M_3 JK2 GP8 III GN 47 are larger than the Bed II kob teeth but probably of the same lineage.

MEASUREMENTS. Measurements on the Bed II fossils are:

	SHK II 1957.579	BK II East P.P.R.1	? MRC II 068/6659
Skull width across posterior side of orbits	–	–	126·8
Length of horn core along its front edge	–	–	240·0
Anteroposterior diameter of horn core at its base	47·6	52·8	41·7
Mediolateral diameter of horn core at its base	48·8	45·9	41·5
Minimum width across lateral surfaces of horn core pedicels	–	110·3	111·7
Width across lateral edges of supraorbital pits	–	60·1	57·1

Measurements on the MNK II specimen are:

Maxilla 103		Mandible 107	
Occlusal length M^1–M^3	50·2	Occlusal length M_1–M_3	53·9
Occlusal length M^2	17·6	Occlusal length M_2	17·4

Lengths and least thicknesses of the limb bones are:

Femur 101	259 × 24·0	Tibia 102	288 × 25·2
Metatarsal 100	184 × 19·4	Metacarpal 105	180 × 20·0

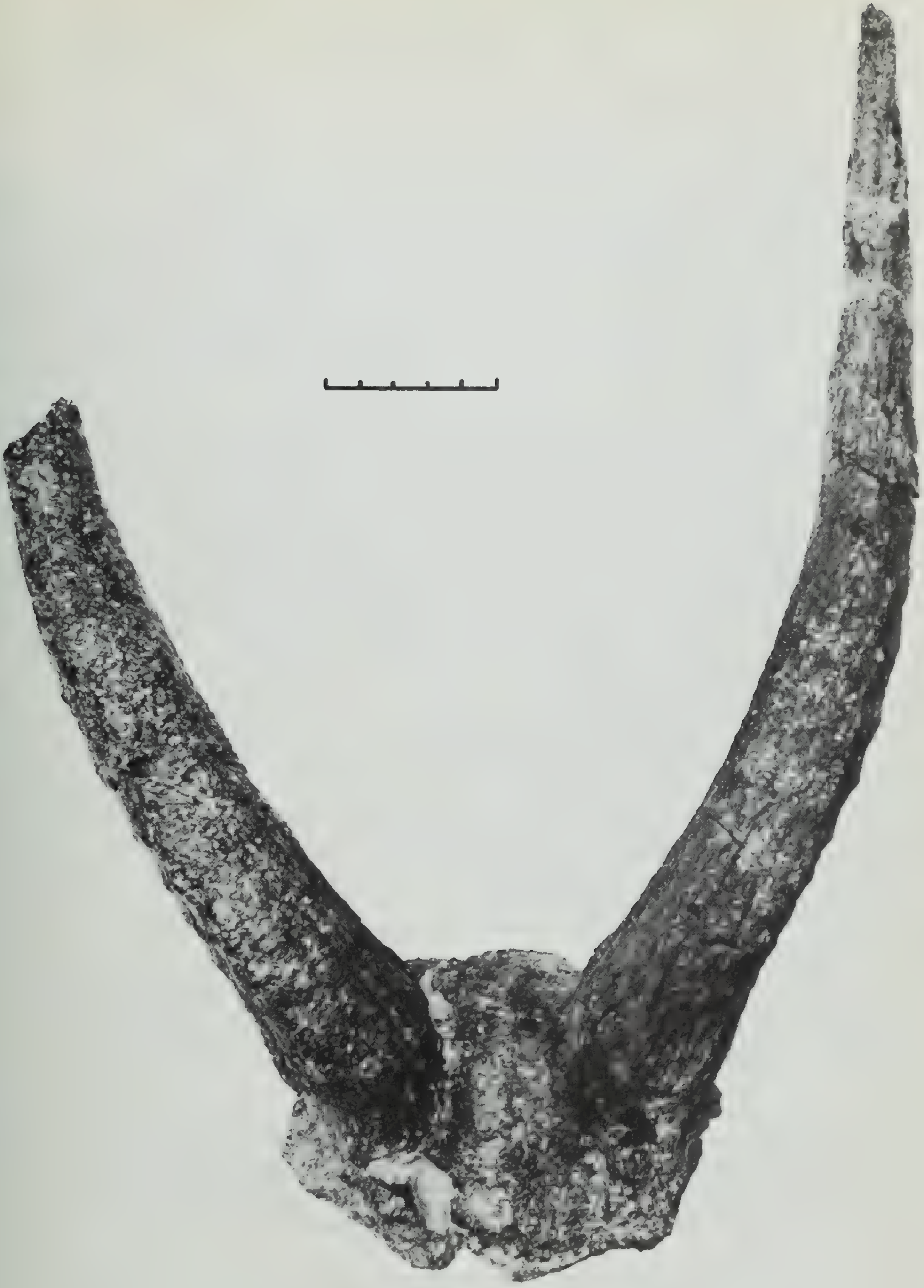


Plate 9 (Scale = 50 mm)

***Kobus kob*.** Dorsal view of frontlet, JK2 GP8 III 068/6694.

Measurements on the Bed III fossils are:

	068/6694	1247
Length of horn core along its front edge	350·0	315·0
Anterposterior diameter at base of horn core	60·6	57·1
Mediolateral diameter at base of horn core	49·2	46·7
Minimum width across lateral surfaces of horn core pedicels	*c.* 122·5	–
Width across lateral edges of supraorbital pits	*c.* 56·8	–

COMPARISONS. The base of a reduncine horn core from Peninj, A67.238.1 (WN 64.227 TMG (lower) USC/MZ), is probably a kob like those of Olduvai Bed II.

The lower half of a left horn core from Rawe BM(NH) M 15936 is from a large kob, and has basal diameters of 54·2 × 48·2. This may have been the basis for the *Redunca* at Rawe recorded by Hopwood (*in* Kent 1942 : 124).

The base of a right horn core from Kanjera BM(NH) M 25628 probably belongs to a kob. It looks very modern with basal backward curvature and a flattened lateral surface. Its basal index is 46·1 × 36·7.

An Upper Pleistocene kob cranium with complete horn cores and associated palate M 15176 from Kazinga Channel, Uganda, was collected by V. E. Fuchs in 1931 (Hopwood 1939 : 314). It closely resembles living kob in the horn cores being long, with some mediolateral compression, inserted close together, curved back from the upright insertions, large and deep postcornual fossae, large supraorbital pits, a close approach of the temporal lines posteriorly, the occipital rather high instead of low and wide, no splaying of the anterior tuberosities of the basioccipital, strong ridges behind the anterior tuberosities, and inflated auditory bullae. The fossil differs from the living kob in its larger size, longer horn cores, the large mastoid without a strong ventral rim and the less evenly rounded occipital edge. Measurements on this cranium are as follows:

Length of horn core along its front edge	*c.* 380·0
Anteroposterior diameter at base of horn core	55·1
Mediolateral diameter at base of horn core	45·3
Minimum width across lateral surfaces of horn core pedicels	105·8
Width across lateral edges of supraorbital pits	51·9
Length from back of frontals to top of occiput	81·5
Maximum braincase width	83·2
Skull width across mastoids immediately behind external auditory meati	105·4
Occipital height from top of foramen magnum to top of occipital crest	46·9
Width across anterior tuberosities of basioccipital	29·0
Width across posterior tuberosities of basioccipital	42·0
Occlusal length M^1–M^3	46·2
Occlusal length M^2	15·8

Kobus kob is definitely known from high levels of the Shungura Formation, for example the Kaalam horn cores P.995-9, P.995-10 and P.996-10, as well as F.203-26 from member K and F.358-9 and F.409-6 from member L. Those from member L are notably large, like those of Olduvai Bed III, but somewhat stockier. There are some doubtful kob horn cores earlier in the Shungura Formation.

Two reduncine horn cores from the later fauna of the Kaiso Formation probably belong to the kob lineage; these are a weathered right horn core base BM(NH) M 12590 from Kaiso village (= cf. *Parmularius altidens* of Cooke & Coryndon 1970 : 212), and a right horn core base from Behanga I which appears to be the M 26622 of Cooke & Coryndon (1970 : 203). A right horn core base from Kanam East Hot Springs, one of two numbered M 15928, is probably also of this lineage.

There must also be mentioned the horn core thought to be BM(NH) M 26623 from Kaiso village, and referred to elsewhere in this paper (p. 414). It has hitherto been taken as alcelaphine, but the lack of a sinus system in the preserved part of its pedicel suggests that it may be a reduncine. Its assignment would thus be ? *Kobus* sp.

Potentially very interesting is the late Pleistocene horn core from Abu Hugar, Sudan, figured by Bate (1951 : text-fig. 3) which Wells (1963 : 303) discussed and identified as cf. *Kobus* sp.

BM(NH) M 21698 is a cast of it. It looks reduncine but is too large and too compressed mediolaterally to fit easily into any living species. The upright insertion in side view, backward curvature and large supraorbital pit suggest that it could be related to *K. kob*, although we have seen nothing like it from elsewhere. Its basal diameters are 61·4 and 40·7 mm.

Reduncine fossils with kob-like characters are well known in the Pinjor Formation of the Siwaliks, and also occur in the preceding Tatrot and Dhok Pathan. The cranium BM(NH) 39559a of *Vishnucobus patulicornis*, already mentioned in the discussion of *Kobus sigmoidalis*, is not unlike a kob. Conspecific pieces would be the holotype frontlet in Calcutta and the holotype cranium of *Indoredunca sterilis* Pilgrim (1939 : 113) also in Calcutta. Other Pinjor reduncines are a little more kob-like and have mostly been classified as *Sivacobus palaeindicus* (Lydekker) by Pilgrim (1939 : 99). We believe that they could be a separate species. They comprise a cranium BM(NH) 39559, and two other more nearly complete skulls with horn cores broken at the bases of their pedicels, M 487 and M 2402, the last one being the holotype. Another male cranium, 17437, is conspecific with the material of *Sivacobus palaeindicus*, although previously regarded as *Vishnucobus patulicornis* (Pilgrim 1939 : 103, mistakenly giving the registered number as 17237). *S. palaeindicus* agrees with *V. patulicornis* in having horn core insertions close together, large supraorbital pits also close together, and strong temporal ridges and fairly small mastoids. However, 39559 has horn cores more massive and with less divergence than 39559a. M 2402 and 17437 differ from the other pieces by their more angled and narrower braincase and by each side of the occipital surface facing laterally as well as backwards. The auditory bullae are large in 17437 but appear to be smaller in M 2402. The closeness of the horn bases and the supraorbital pits to the mid-line of the skull and the large size of the supraorbital pits are much as one might expect in kob ancestors, and M 2402 and 17437 are still more kob-like in their narrower and more angled braincases. However, we do not know whether even the more kob-like examples are ancestral to kobs. They may only be earlier members of the same lineage as *Vishnucobus patulicornis* and kob-like by reason of their relative primitiveness. Could Indian populations of antelopes as closely associated with proximity to water as the reduncines have been connected across Arabia with African populations as late as Pinjor times? Does the retention of strong temporal ridges on the cranial roofs of the Pinjor reduncines suggest that they are earlier than *Kobus sigmoidalis* as known back to Shungura member C, or that they are an endemic Indian group? If they were endemic, the chances would be lessened that the were congeneric with *Kobus*.

Gangicobus asinalis Pilgrim (1939 : 111) and *Sivadenota biforis* Pilgrim (1939 : 105) were founded for two hornless female skulls, BM(NH) 36673 and 39569 respectively, but it is impossible to decide to which of the above two species, *Vishnucobus patulicornis* and *Sivacobus palaeindicus*, they should be allocated. It is interesting that M 487 and M 2402, but not the female skulls, retain small preorbital fossae which have disappeared in living reduncines. These fossae are further reduced in the Omo *Menelikia lyrocera* and absent in the females of the Olduvai *Kobus sigmoidalis* and the Bed II kob, but the condition in other fossil reduncines is unknown. The occurrence of the Siwaliks reduncines in the same area as earlier abundant boselaphines and their strong temporal ridges suggest that they could have a boselaphine ancestry. The Tatrot and Dhok Pathan reduncines are smaller and less adequately preserved, but presumably they were ancestral to those of the Pinjor. No Siwaliks reduncines resemble *Reduncа* or *Menelikia*.

Baard's Quarry at Langebaanweg, South Africa, yielded some horn cores wrongly assigned by Gentry (*in* Hendey 1970a : 115) to *Redunca ancystrocera*. They are only a little mediolaterally compressed, inserted fairly obliquely and divergently, have slight backwards curvature, a flattened lateral surface, no transverse ridges, and moderate-sized but very deep postcornual fossae. They are very like the Tatrot and Dhok Pathan reduncines except that their supraorbital pits are smaller.

Genus ***REDUNCA*** H. Smith 1827

TYPE SPECIES. *Redunca redunca* (Pallas 1767).

GENERIC DIAGNOSIS. Reduncines frequently smaller than *Kobus*; skulls low and wide; horn cores of variable length but always with an upwards curvature which is forwardly concave from the base, with little mediolateral compression, and often with a posteromedial or medial flattened surface near the base; frontals without internal sinuses; anterior tuberosities of the basioccipital very large and outwardly splayed.

REMARKS. *Redunca* is a smaller and less diversely adapted genus than *Kobus* and this allows a diagnosis with more characters.

Redunca sp.

Remains of *Redunca* are very scarce at Olduvai. Reduncine right lower molars DK I 067/4085 and FLKN I 067/185 are small enough to fit *Redunca*. A left upper molar JK2 III A.1438N is also probably *Redunca*, but could just possibly be a kob.

COMPARISONS. Complete and fragmentary left horn cores BM(NH) M 26930 and M 26931 from Kanam East and an immature right one M 26932 from Kanam belong to *Redunca*. M 26930 retains the midfrontals suture, is set obliquely in side view, has a flattened posteromedial surface near its base and is short and little divergent. All three horn cores are distinguishable from *R. redunca* only by being less curved in side view. A mandibular fragment with a left lower molar M 15934 from Kanam Central is of *Redunca* size. The more complete of two horn cores numbered M 15928 from Kanam East Hot Springs differs from M 26930 by having less anteroposterior compression and a more medial position of the flattened posteromedial surface. These characters look primitive and M 15928 may be assigned to *Redunca* ? *darti* (see below), yet the Hot Springs fossils are thought to derive from the Rawe beds later than the Kanam beds (Kent 1942 : 124).

M 25634 is a right horn core base of *R. redunca* from Kanjera, but it appears to be little fossilized. M 25713 is a little-fossilized left upper molar of *Redunca* size from Kanjera.

Teeth small enough for *Redunca* are scarce in the Shungura Formation, Omo, e.g. left lower molar L.32-179 from member C and left lower premolar L.209-4 from member E.

Reduncine molars M 26620 and M 26621 (Cooke and Coryndon 1970 : 203) from the later Kaiso faunal assemblage at the Behanga locality are small enough to belong to *Redunca*, but of the two further teeth from Makusa mentioned by these authors, one is a larger reduncine and one is an alcelaphine.

In contrast with Olduvai, remains of *Redunca* are fairly common in South Africa and occur at several fossil sites. *R. arundinum* is the commonest antelope at Melkbos (Hendey 1968 : 110) and similar remains occur at Swartklip (Hendey & Hendey 1968 : 51; pl. 2). At Elandsfontein parts of a skull 20039, several frontlets, horn cores and mandibles represent the apparent ancestor of living *R. arundinum*, but have horn cores more anteroposteriorly compressed, less divergent and possibly shorter. The short and little-divergent horn cores happen to resemble *R. redunca*, but since the occipital surface has a more rounded edge like *R. arundinum* and since *R. redunca* is a more northern form, this probably shows only that earlier members of the *arundinum* lineage were less remote from *redunca* than is the living *arundinum*.

The Elandsfontein subspecies of *R. arundinum* is possibly descended from the Makapansgat Limeworks *R. darti* Wells & Cooke (1956 : 17, figs 7–9). This extinct species differs from *R. redunca* and *R. arundinum* in its horn cores being less oblique in side view, and the posteromedial flattened surface lying more medial than posterior. It differs from *R. fulvorufula* in its larger size and horn cores relatively larger, more divergent, more obliquely inserted, and with posteromedial or more medial flattenings on the surface. Unlike any living *Redunca* it probably had a small preorbital fossa, as seen on the incomplete skull BPI M.690 and partial face M.2798. Whether *R. darti*, being tentatively ancestral to *R. arundinum*, was also ancestral to *R. redunca* is not known. The Kanam East Hot Springs horn core BM(NH) M 15928, mentioned above, is similar to *R. darti*.

Arambourg (1938 : 44; pl. 8, figs 1–2) recorded *Redunca redunca* from the late Pleistocene and early Holocene of north-west Africa. The horn cores of similar age figured as *Antilope* (*Oegoceros*) *selenocera* Pomel (1895 : pl. 6, figs 1–3) are also assignable to *R. redunca*. They do not represent a waterbuck as Joleaud (1936 : 179) believed. Arambourg (1957 : 51) pointed out that the frontlet *A.* (*Dorcas*) *triquetricornis* Pomel (1895 : 28; pl. 11, figs 1–2) is also a *Redunca* which most probably went with the teeth called *A.* (*Nagor*) *maupasii* Pomel (1895: 38; pl. 10, figs 1–11). The size, inclination and cross-sections of the *Redunca* horn cores figured by Pomel forbid their assignment to *R. fulvorufula*. Coppens (1971 : 53) refers to a *Redunca* from Villafranchian-equivalent deposits of Garaet Ichkeul and Hamada Damous, Tunisia, but the details are to be published later.

Redunca ancystrocera Arambourg (1947 : 416, fig. 62; pl. 29, fig. 4; pl. 31, figs 2, 4, 4a) from the Shungura Formation, Omo, is ill-suited as a *Redunca* on account of its larger size and horn cores often with posterolateral keels and flat lateral surfaces. It seems better classified as a species of *Kobus*. Its horn core characters of low insertion angle, great divergence and pronounced upwards and forwards curvature at the tips resemble living *Redunca* but are unlike the more primitive fossil species *R. darti*.

The Laetolil right horn core which Dietrich (1950: 36; pl. 2, fig. 21) called 'Reduncini gen. et sp. indet.' is more likely to be alcelaphine (see p. 382).

Genus *THALEROCEROS* Reck 1935

1935 *Thaleroceros* Reck : 218.

Type species. *Thaleroceros radiciformis* Reck 1935.

Generic diagnosis. There is only one species in the genus.

Thaleroceros radiciformis Reck 1935

1935 *Thaleroceros radiciformis* Reck : 218, fig. 2.
1937 *Thaleroceros radiciformis* Reck : 142; pl. 8.
1950 *Alcelaphus radiciformis* Dietrich : 15, 33.

Diagnosis. A large antelope; horn cores fairly long but very massive, not very compressed mediolaterally, without a flattened lateral surface, without keels or transverse ridges, diverging very little, with an upwards and forwardly concave curvature from the base, and a sudden diminution of cross-sectional area near their tip; horn core pedicels united to form a single massive structure without internal sinuses and with paired protuberances anteriorly just below the horn core bases; postcornual fossae poorly marked; orbital rims slightly projecting; supraorbital pits small and elongated; frontals internally hollowed at the level of the supraorbital pits.

Holotype. The holotype and only known specimen is in Munich, where it has survived the Second World War. It is a frontlet with right horn core, marked 'VI 306, 1931 II 101'.

Horizon. Reck (1937 : 138) thought the fossil came from Olduvai Bed IV. R. L. Hay (personal communication, September 1969) identified matrix from it as 'a pale brown sandy clay, not at all diagnostic in locating the specimen's horizon. It could have come either from Bed II (probably the upper part) or from Bed IV.'

Remarks. The holotype has an almost complete right horn core, but with some plaster restoration near its tip on the medial side and an artificial hole posteromedially near its base. Both supraorbital pits, the upper parts of both orbits, the anterodorsal part of the braincase roof and a small part of the right lateral wall are preserved. The left horn core has been restored in plaster.

The pedicel is higher at the front than at the back, and there is a shallow concavity below and between the anterior protuberances. Posteromedial breakage on the right side of the horn pedicel shows that it is spongy within, and the hollowing of the frontals is therefore restricted to a more anterior level, which is unlike the alcelaphine condition. The posteromedial hole near the base of the right horn core shows that the horn core itself is spongy within, and therefore unlike Caprini. The right protuberance on the pedicel is larger than the left one, and the base of the right side of the pedicel is more swollen posteriorly. Possibly the missing left horn core was smaller than the right one, and the animal perhaps old.

The left horn core 1955 P.P.F.4 from the surface of FLK tentatively assigned by Leakey (1965: 65; pl. 88) to *T. radiciformis* is not this species but an unidentified alcelaphine (p. 393).

MEASUREMENTS. Measurements on the frontlet of *Thaleroceros radiciformis* are:

Length of horn core along its front edge	306·0
Anteroposterior diameter of horn core at its base	121·0
Distance from horn core tip to centre of protuberance	254·0
Minimum width across horn core pedicel	119·4
Width across lateral edges of supraorbital pits	67·0
Maximum width across fossil and restored horn core bases	*c.* 198·0

COMPARISONS. *T. radiciformis* shows a distant resemblance to *Kobus ancystrocera* (Arambourg 1947 : 416) from the Shungura Formation, Omo, in its forwardly curved horn core tip and upright horn core pedicel, and a horn core base of the latter, L1-153 from member B of the Shungura Formation, Omo, even has a localized protuberance at the top of its pedicel. It is possible that *T. radiciformis* is a very specialized descendant of *K. ancystrocera*, but it is much larger, the pedicel is united, and the horn cores do not diverge so strongly. Possible intermediates are a complete right and part of the left of a pair of horn cores, BM(NH) M 15925, from Kanam. They are supposed to have come from a site called 'Museum Cliff'. They are considerably larger than *K. ancystrocera* and less mediolaterally compressed than either *K. ancystrocera* or *T. radiciformis*. Their horn core index is 70·2 × 60·2 mm. However, they do not attain the size of *T. radiciformis*, and their pedicels have not become united, so they are a good intermediate stage. M 15927, labelled '*Cobus* sp.', from Kanam East Hot Springs is another piece of horn core which is very like the pair M 15925. Reck (1937 : 142) had noticed similarities between *T. radiciformis* and the reduncines, but was deterred from suggesting a relationship by the huge united pedicel and by the internal hollowing of the frontals.

Tribe **HIPPOTRAGINI**

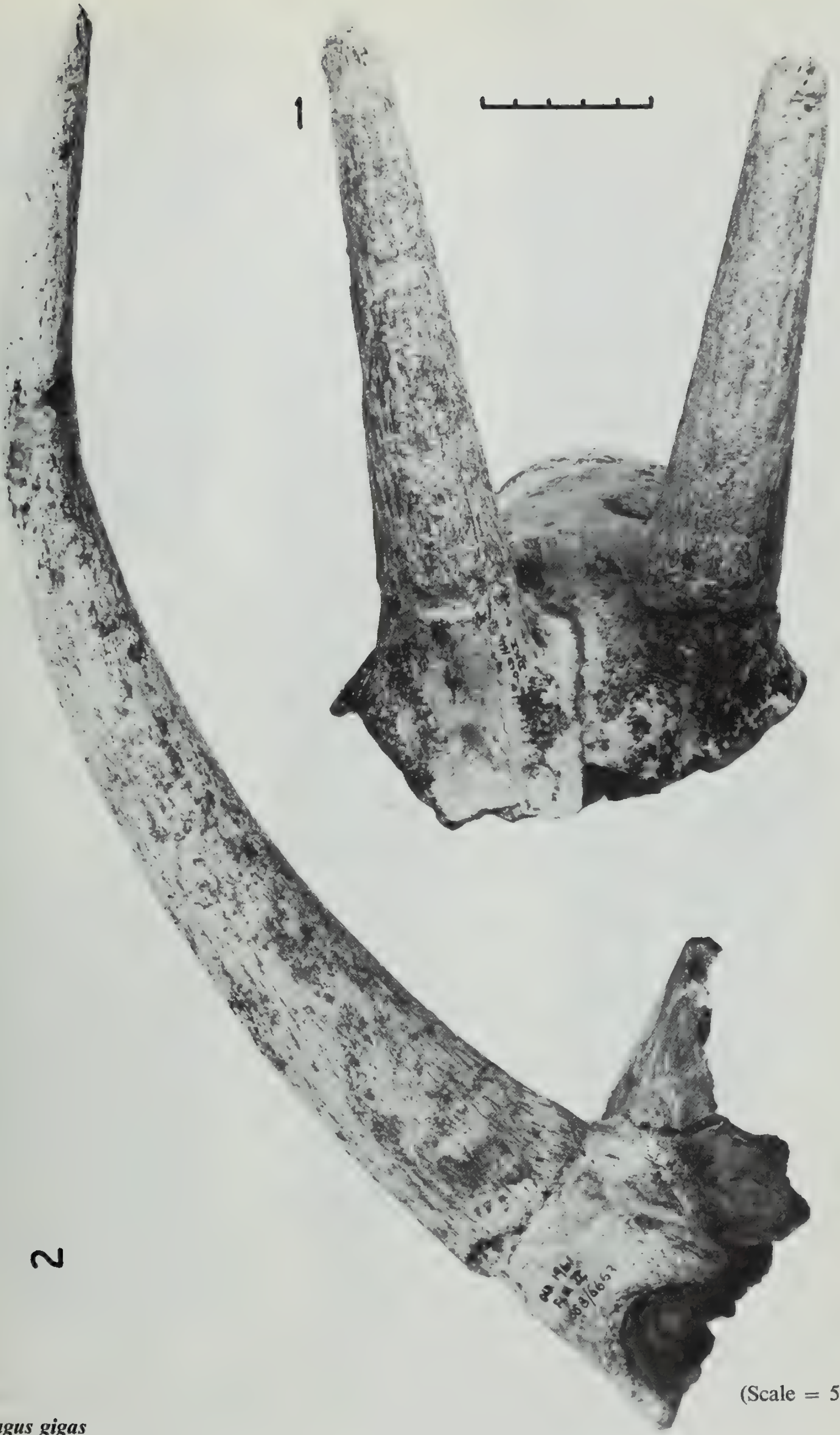
The living Hippotragini comprise the sable, roan, oryx and addax. The first lives in woodland, the second in clearings or along the edges of woodland, the oryx in drier habitats and the addax in the Sahara desert. They are large, rather stocky, mainly grazing (except the addax) antelopes with large, unkeeled horns (spiralled in the addax) and moderately hypsodont teeth. The distinctive skulls characters are: horn cores moderate to long, horn cores not very divergent and without keels or transverse ridges, horn core pedicels hollowed, both sexes with horns. Postcornual fossae shallow when present, braincase long, midfrontals suture moderately complicated, parietofrontals suture straight and not very complicated, temporal lines not approaching very closely, ethmoidal fissure present, infraorbital foramen fairly high over the P^2–P^3 junction, premaxillae with a short contact along the sides of the nasals, nasals without lateral flanges anteriorly, median indentation at the back of the palate more or less level with the lateral ones, mastoid exposure moderate to large, foramina ovalia large, auditory bullae moderately large. Teeth large relative to the jaw size, upper molars with basal pillars, lower molars with goat folds anteriorly, P_4s without metaconid and paraconid fusion to form a complete medial wall at the front of the tooth, and mandibles with deep horizontal rami.

Hippotragus leucophaeus (Pallas 1766), the blaauwbok of southern South Africa, was the smallest of the three *Hippotragus* species. It became extinct at the end of the 18th century. It is the type species of *Hippotragus*.

Hippotragus equinus (Desmarest 1804) is the roan antelope of much of Africa south of the Sahara.

Hippotragus niger (Harris 1838), the sable antelope of East and South Africa, differs from *H. equinus* in relatively larger, longer, more mediolaterally compressed and more uprightly inserted horn cores, frontals more raised between the horn core bases, narrower skull width across the orbits and a shorter braincase which is more bent on the facial axis.

Oryx gazella (Linnaeus 1758), the gemsbok and beisa of South and East Africa, differs from living *Hippotragus* in having a lower and wider skull, and straighter and less compressed horn cores, inserted very obliquely, further behind the orbits and wider apart. The gemsbok has larger teeth than the beisa.



(Scale = 50 mm)

Plate 10

Hippotragus gigas

Fig. 1 Anterior view of immature partial cranium, DK I 067/5496.

Fig. 2 Lateral view of left horn core, FLK II 1961.068/6663.

Oryx dammah (Cretzschmar 1826), the scimitar oryx of west Africa, has more curved horn cores than other *Oryx*.

Oryx leucoryx (Pallas 1777) is the slightly smaller Arabian oryx.

Addax nasomaculatus (Blainville 1816) is the spiral-horned addax which lives in parts of the Sahara desert. It is still more adapted to life in arid regions than oryxes, and no fossils are known.

Genus ***HIPPOTRAGUS*** Sundevall 1846

Type species. *Hippotragus leucophaeus* (Pallas 1766).

Generic diagnosis. Horn cores mediolaterally compressed, strongly curved backwards, inserted uprightly above the orbits and closer together than in *Oryx*; ethmoidal fissures blocked by bone internally; nasals more domed than in *Oryx*; mastoid facing partly laterally as well as backwards; longitudinal ridges behind the anterior tuberosities of the basioccipital are stronger than in *Oryx*; lower molars with stronger goat folds than in *Oryx*.

Hippotragus gigas L. S. B. Leakey 1965

1942 *Hippotragus equinus* Hopwood (*in* Kent) : 126.
1965 *Hippotragus gigas* Leakey : 49; pls 56, 58–61.
1965 *Hippotragus* cf. *equinus* (in part) Leakey : 51.
1965 Bovinae indet. Leakey : 66(a); pls 89–90.
1965 cf. Alcelaphini Leakey : 66(c).

Diagnosis. A species larger than living *Hippotragus* at least during part of the Olduvai sequence; males with very large and long horn cores; horn cores less mediolaterally compressed than in the sable and probably less than in the roan; a shorter basioccipital than in living *Hippotragus*; braincase proportions low and wide as in the roan rather than high and narrow like the sable, but less long than in the roan; frontals not raised between the horn corn bases as in the sable but resembling the roan; outbowings not accentuated nor localized on lateral walls of upper molars or medial walls of lowers; upper molars without large Y-shaped basal pillars; lower molars with large goat folds as in living *Hippotragus* but without pinching of the lateral lobes; premolar rows as short and P_2s as small as in *Oryx*.

Several crania from Elandsfontein are of a large hippotragine which seems conspecific with *H. gigas* and from this material a further character can be added to the diagnosis: large foramina ovalia.

Holotype. Incomplete cranium with both horn cores F.3662 068/5812 P.P.T.2 in the Nairobi collections.

Horizon. The holotype comes from Bed II, Olduvai. According to R. L. Hay (personal communication, September 1973) a small remaining piece of matrix was limestone with sand-sized volcanic detritus indicating an origin above the Lemuta Member, probably in the eastern half of the Main Gorge. Other specimens are moderately common in Beds I–III. The species is known from Kanjera and Peninj, from the Chiwondo Beds in the Karonga District of Malawi, and in South Africa from Makapansgat Limeworks, Elandsfontein and possibly Florisbad.

Remarks. *H. gigas* is the only species of *Hippotragus* at Olduvai. It had a long history in East Africa and continued into the late Pleistocene in South Africa. The later stages were certainly not ancestral to living *Hippotragus*, but we do not know when the lineages separated. The more complete remains from Olduvai are a juvenile cranium with both horn cores DK I 067/5496 (Pl. 10, fig. 1), a cranium with horn cores, both mandibles (Pl. 11, fig. 3) and parts of the maxillae FLKNN I 608 (thought to be possibly alcelaphine by Leakey (1965 : 66(c)), the female paratype cranium with horn cores 1957.56 P.P.T.3 from VEK at the top of Bed I, a complete left horn core and part of the braincase 1961.068/6663 from FLK middle Bed II (Pl. 10, fig. 2), the back of a skull TK II 067/5310, a complete left horn core BK II 1963.3042, and a frontlet with the basal part of the right horn core F.3014 of unknown stratigraphic position (Leakey 1965 : 66(a); pls 89–90). Specimens in London are the lower part of a left horn core BM(NH) M 14530 from Bed I

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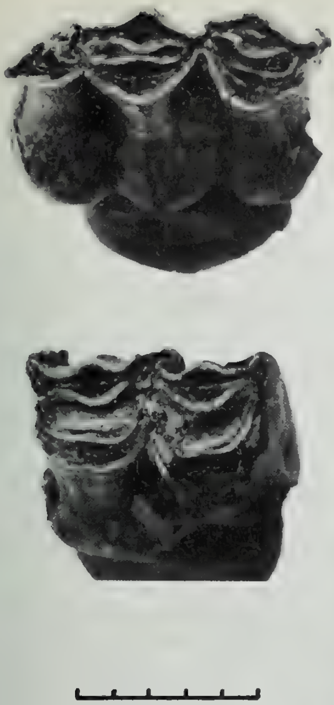

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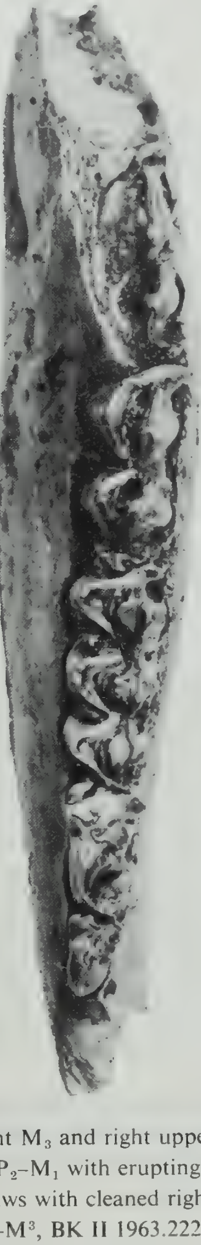

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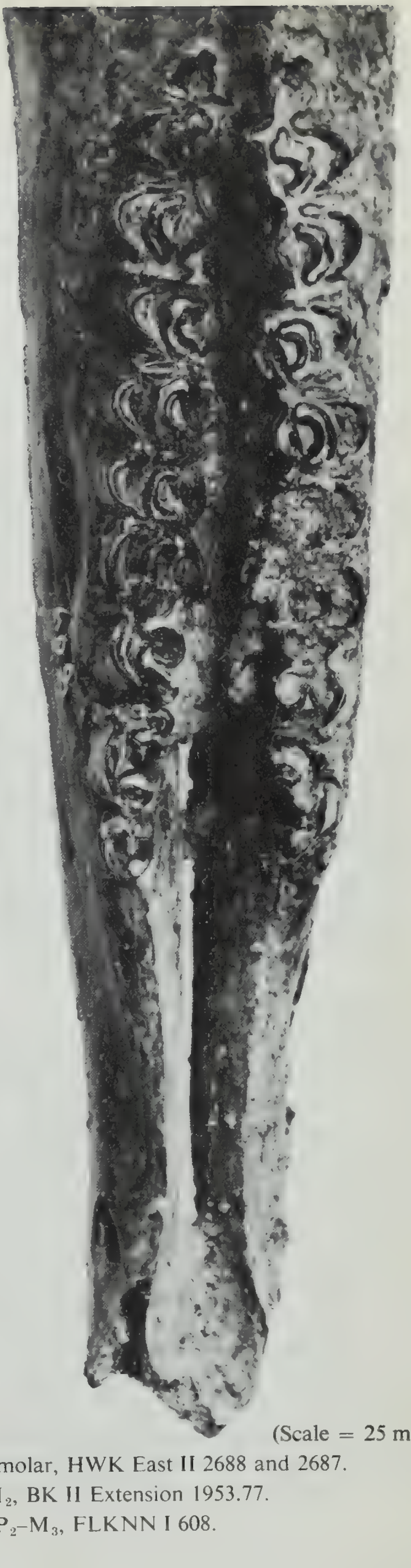

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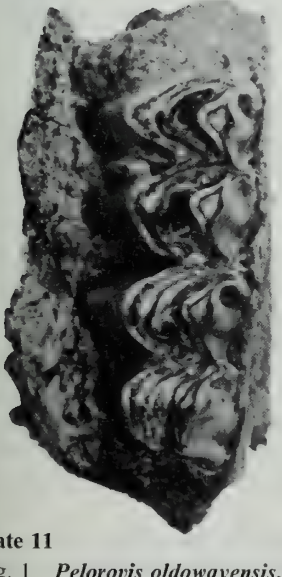

Plate 11 (Scale = 25 mm)

Fig. 1 ***Pelorovis oldowayensis.*** Right M_3 and right upper molar, HWK East II 2688 and 2687.

Fig. 2 ***Syncerus acoelotus.*** Right dP_2–M_1 with erupting M_2, BK II Extension 1953.77.

Fig. 3 ***Hippotragus gigas.*** Lower jaws with cleaned right P_2–M_3, FLKNN I 608.

Fig. 4 ***Hippotragus gigas.*** Left M^2–M^3, BK II 1963.2226.

and a right horn core base M 21449 from Bed II (written on the horn core and in the register) or Bed I (written on the label), both found in 1932 and recorded as *H.* cf. *equinus* by Leakey (1965: 51), a right horn core M 21448 from Bed II in 1931 (Leakey 1965: 50; pl. 61), a left horn core M 29425 from the surface of GHTK II in 1935 and the lower part of a left horn core M 29424. Possibly belonging to this species are pieces of horn core M 14541 and M 14533 both found in Bed I in 1932.

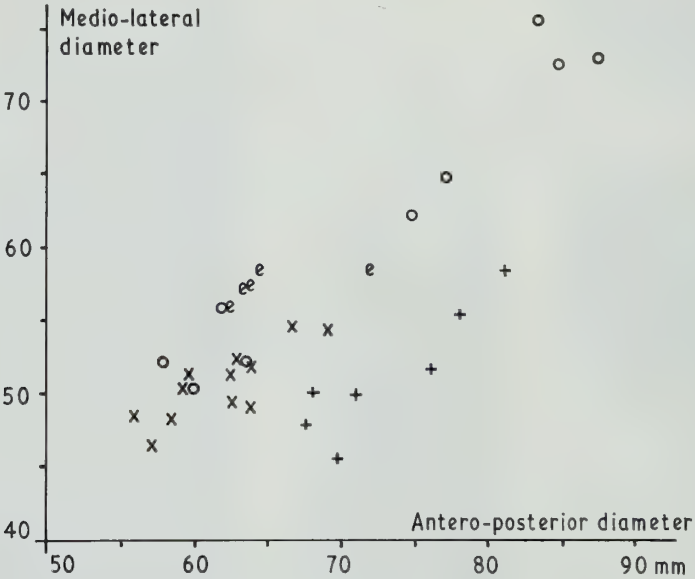

Fig. 14 Horn core dimensions of *Hippotragus*.

o = *H. gigas* from Olduvai Gorge, *e* = *H. gigas* from Elandsfontein, x = *H. equinus*, + = *H. niger*.

All readings are from males or individuals which cannot be reliably distinguished from males. *H. gigas* shows great variations in size, although its lowest reading, BK II East 1953 P.P.R.5, is probably not adult.

The holotype cranium is definitely larger than either of the living species and it has horn cores larger and longer than those of the roan, both absolutely and in relation to skull size. The dimensions of the horn cores probably exceed those of all but the largest sable. The other Olduvai horn cores are also larger and longer than in living species, and the young cranium from DK I is also rather large. The horn cores of *H. gigas* are less compressed than in sable and probably than in roan (Fig. 14), little divergent in anterior view (except in 608), inserted above the back of the orbits, and lack a flattened lateral surface, keels and transverse ridges. The various horn cores from Olduvai are consistent with the supposition that the adult females and the young of both sexes have more obliquely inserted horn cores than adult males and that those of females have less backward curvature than males. This is what happens in living *Hippotragus*. Thus the horn cores of 067/5496, which is young, are inserted obliquely; those of 608, probably a female, are inserted obliquely and lack much backward curvature; those of the paratype, also probably a female, also lack much backward curvature but are not inserted very obliquely; that of 068/6663 is obliquely inserted but quite strongly curved backwards and could have belonged to a male whose horns had not yet attained full size.

There seem to be no postcornual fossae in *H. gigas*. That part of the frontals constituting the horn core bases is clearly hollowed, but as seen on the holotype and probably the paratype and 067/6663 the frontals are not raised between the horn core bases as in the sable but are like the

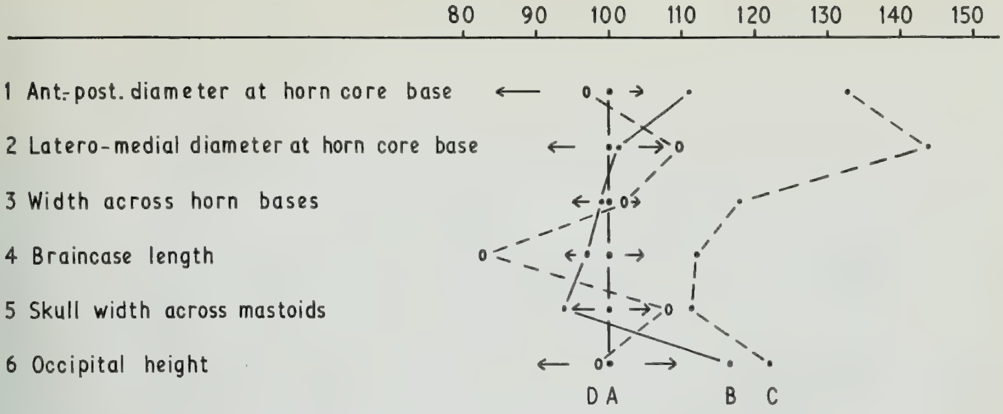

Fig. 15 Percentage diagram of skull measurements in *Hippotragus*.

A = standard line at 100% for mean of 12 male *H. equinus*, B = mean readings for 7 male *H. niger*, C = *H. gigas* holotype, D = mean readings for 3 *H. gigas* from Elandsfontein.

Horizontal arrows show the standard deviations for *H. equinus*. Braincase length is measured from the back of the frontals to the occipital top.

roan. The supraorbital pits are small and about as wide apart as in living hippotragines. In side view the tops of the orbits are close under the tops of the horn core pedicels. The midfrontal and parietofrontal sutures are complicated and there is but little central indentation of the parietofrontal suture.

The braincase sides of *H. gigas* are parallel or widen posteriorly. The braincase proportions, as shown by the holotype, paratype and 067/5496, are relatively wide like the roan but relatively less long (Fig. 15); that of 608 appears still shorter but has been considerably crushed anteroposteriorly. The occipital surface faces backwards and the median occipital ridge is slightly developed. On the holotype and 067/5496, though not on 067/5310, there are shallow hollowings on either side of the median vertical line at the top of the occipital surface which are not convincingly present in either of the living species, though there may be indications in the roan. The nuchal crest is moderately prominent on the holotype and 067/5310, though this is not noticeably

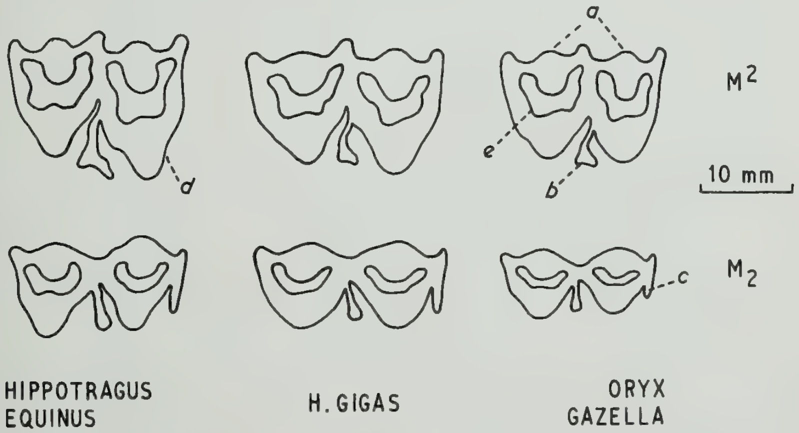

Fig. 16 Occlusal surfaces of right upper and lower molars in some hippotragine species. The anterior direction lies to the right of the page. *a* = ribs, *b* = basal pillar, *c* = goat fold, *d* = constriction of lobe, *e* = outline of central cavities.

different from the living species. The basioccipitals of 608, 067/5310, the paratype and probably the holotype are shorter than in the living species. There is very little of a central longitudinal groove on the basioccipitals. The anterior tuberosities of the basioccipital are almost as wide as the posterior ones. The anterior tuberosities of 608, 067/5310 and the paratype can be seen to be localized, as in oryx rather than sable or roan. The mastoid exposure in *H. gigas* is large.

All the hippotragine teeth at Olduvai can be taken as belonging to *Hippotragus gigas* (Fig. 16). In this connection, the skull FLKNN I 608 is important in providing the only association between dentitions and horn cores, and one has to be certain of the specific identity of 608. It is likely that distortion has forced the braincase roof close against the back of the horn cores, making them appear very obliquely inserted as in oryxes. However, 608 cannot be an oryx because the horn cores are too large, they are too backwardly curved, they do not taper rapidly above the base like a fossil oryx horn core FLK I G.390, the pedicel top is probably too far above the orbit and the orbital rim probably projects too little. The skull can therefore be taken as *H. gigas*.

The teeth of *Hippotragus gigas* are about the size of living *H. equinus* or slightly larger at least from middle Bed II times onwards. They resemble living *Hippotragus* in the large size of the goat fold, but otherwise they are more like *Oryx* in the poorly emphasized outbowings of the lateral wall of the upper molars and the medial wall of the lowers, the lack of large Y-shaped basal pillars on the upper molars, the lower molars without pinching of the lateral lobes, the shorter premolar row, and perhaps in the less complicated outline of the central cavities. Thus the teeth of *H. gigas* are more primitive than in living roan or sable, and with premolar rows as short as in *Oryx* (Fig. 17) they are almost indistinguishable from oryx.

There is little definite sign that these characters are becoming more advanced in the sparse fossils from middle or upper Bed II. However, the maxilla BK II 1963.2226 (Pl. 11, fig. 4) does have upper molars with rather localized and accentuated ribs between the styles. In Bed III the lower molar JK2 A.2838 is still primitive, but JK2 A.3028 begins to show some constriction of the

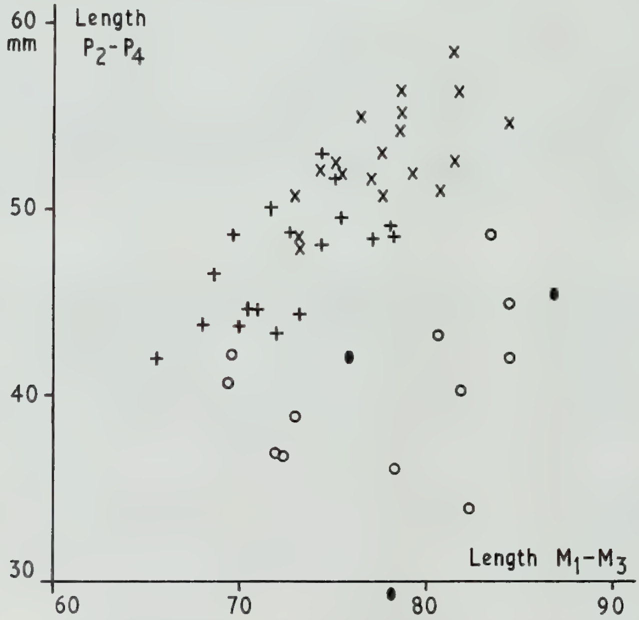

Fig. 17 Proportions of lower premolar and molar rows in some hippotragines.
o = *Oryx gazella*, + = *Hippotragus niger*, x = *H. equinus*.
Solid circles show *H. gigas*, the smaller one being FLKNN I 608 from Olduvai, and the larger the mean of 2 premolar rows and 6 molar rows from Elandsfontein. A molar row reading for *H. gigas* FLK I 1960.067/1097 is also shown below the horizontal axis.

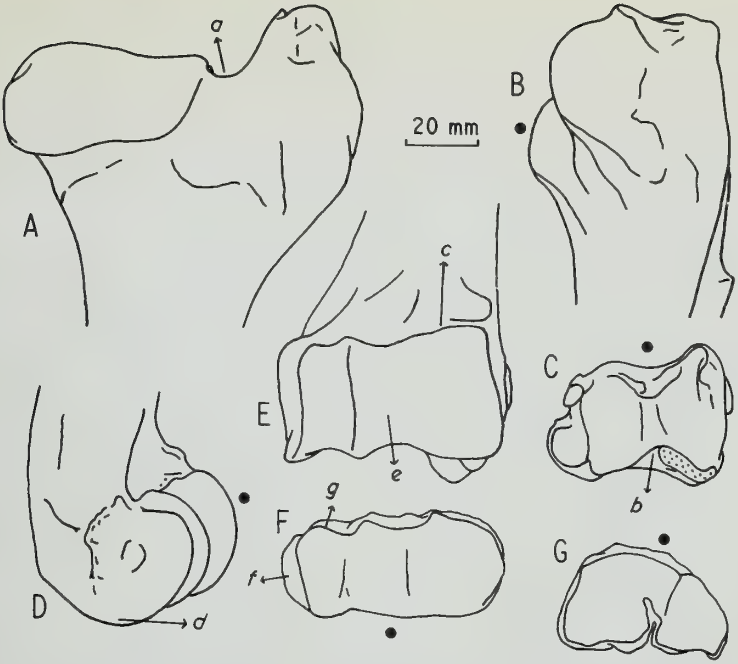

Fig. 18 Limb bones of Olduvai *Hippotragus*. (Solid dots show anterior sides.)

A, B. Anterior and lateral views of proximal left femur FLKNN I 800.
C. Distal articular surface of right tibia of same skeleton.
D, E. Lateral and anterior views of distal right humerus of same skeleton.
F. Proximal articular surface of right radius of same skeleton.
G. Proximal articular surface of right metacarpal FLKNN I 960.

a = hollow between great trochanter and articular head which is less deep than in alcelaphines.
b = shallow rear indentation into distal articular surface,
c = no indentation at top of medial condyle,
d = rounded ventral edge of lateral side,
e = medial groove insufficiently deep to match alcelaphines,
f = small lateral tubercle,
g = back of lateral facet set posteriorly.

These characters may be compared with the alcelaphine limb bones shown in Fig. 23, p. 374.

lateral lobes, while the right lower molar fragment from JK2 has a localized and accentuated rib on its medial wall. We need more evidence about whether or not *H. gigas* teeth become more advanced later in the Pleistocene. (A deciduous P^4, BK II 1952.167, is so markedly advanced that one must doubt whether it is contemporary with its alleged horizon.)

It is rather difficult to distinguish teeth of *Hippotragus gigas* from those of the bovine *Syncerus acoelotus* or its ancestor in Olduvai Beds I and II. Some general guides can be laid down. Hippotragine teeth can be expected to be a little smaller and the premolar rows very short. The lower molars may have less narrowed lateral lobes, less pronounced outbowings on the medial walls, and goat folds which extend down to the neck of the tooth. Bovini too may occasionally have goat folds, as in BK II 1953.067/5230, but they are smaller and disappear before the tooth is completely worn down. The hippotragine P_4 has a large bulbous metaconid (more so than in living *Hippotragus*) and there is no tendency to fuse paraconid and metaconid. The identification of hippotragine upper molars is still more difficult, but one can look for less mediolateral width lower down and the correlated character of less curved central cavities.

H. gigas seems closer to the roan than to the sable in the low and wide braincase, not very compressed horn cores, projecting orbital rims and lack of raised frontals between the horn core bases. It differs from the roan in the much larger horn cores, probably less long braincase, sometimes stronger temporal lines, shorter basioccipital, less development of longitudinal ridges behind the anterior tuberosities of the basioccipital and larger foramina ovalia. Morphologically, *H. gigas* could be ancestral to either or both living species of *Hippotragus*, except that its very short premolar row would be a problem. It is entirely possible that some populations of *H. gigas* gave rise to living *Hippotragus*, while elsewhere the species *gigas* lived on.

The partial skeleton of a large bovid was found at the base of the tripartite level of FLKNN I in 1961. This is slightly higher in the sequence than level 1 of FLKNN I and is overlain by Tuff ID (M. D. Leakey 1971b : fig. 19). The skeleton (Figs 18 and 19) consists of a complete right humerus 800M, complete right radius 800D and right ulna 800P, complete right tibia 800, complete left femur 800A, most of the pelvic girdle 800H–J, right calcaneum 800L and several vertebrae and ribs. The remains are those of a hippotragine and are distinguished from a similar-sized large alcelaphine (though with more difficulty than might be expected from such complete material) by the following characters: in anterior view the hollowing between the great trochanter and articular head of the femur is not quite deep enough, the radius and tibia are too short, there is a middle patellar groove at the top of the cnemial crest of the tibia, the rear indentation into the distal articular surface of the tibia is too shallow, there is no indentation on top of the medial condyle distally on the humerus and no V-projection distally on its lateral surface, the medial groove distally on the humerus is insufficiently deep, and on the radius the lateral tubercle is too small and the back of the lateral facet is not set anteriorly.

The anteroposteriorly long lateral part of the femur articular head and lack of extreme forward extension of the great trochanter can be seen in living *Oryx* rather than *Hippotragus*. The extreme forward projection of the medial side of the patellar fossa on the femur and the raising of the lateral edge of the lateral facet on the tibia are also more *Oryx*-like. The skeleton is probably *Hippotragus gigas* but shows some *Oryx*-like features. If it is indeed *H. gigas*, then it is not very large (Fig. 19) and the tibia and radius are relatively short in comparison with both living *Hippotragus* species. Further comments on hippotragine limb bones can be found in the account of the FLKNN site, in Part II.

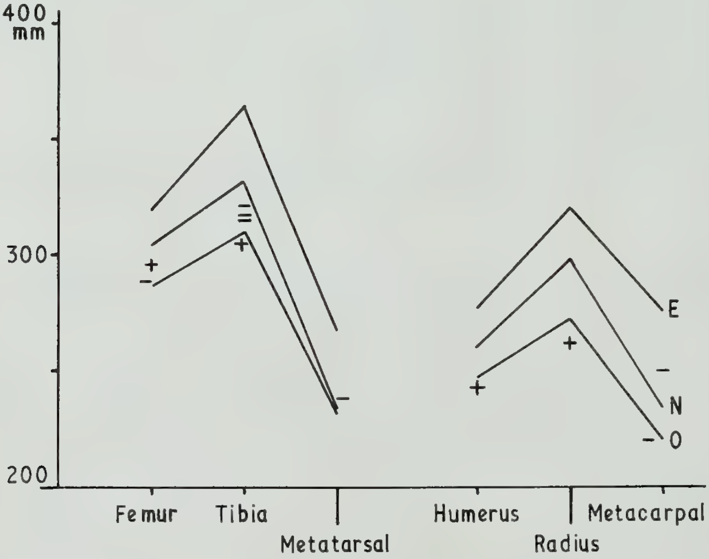

Fig. 19 Lengths of limb bones in Hippotragini. E = mean of 2 *Hippotragus equinus*, N = mean of 4 *H. niger*, O = mean of 3 *Oryx gazella*. Horizontal dashes indicate Hippotragini from Olduvai Bed I, and the crosses show the skeleton FLKNN I 800.

MEASUREMENTS. Measurements on the crania of *H. gigas* are:

	DK I 067/5496 (immature)	FLKNN I 608	VEK I 56 P.P.T.3	Bed II 068/5812
Length of horn core along its front edge	180+	–	*c.* 475·0	*c.* 640·0
Anteroposterior diameter of horn core at its base	47·6	55·3	66·9	87·6
Mediolateral diameter of horn core at its base	42·0	45·6	51·7	73·0
Minimum width across lateral surfaces of horn core pedicels	119·7	137·0	154·0	158·0
Width across lateral edges of supraorbital pits	68·3	–	–	–
Length from back of frontals to top of occiput	87·2	–	89·1	115·5
Length from midfrontal suture at the level of the supraorbital pits to top of occiput	158·0	–	–	213·0
Maximum braincase width	92·0	–	102·0	–
Skull width at mastoids immediately behind external auditory meati	120·0	–	–	148·0
Occipital height from top of foramen magnum to top of occipital crest	–	–	–	68·8
Width of anterior tuberosities of basioccipital	–	42·6	–	–
Width of posterior tuberosities of basioccipital	–	46·6	63·0	54·9
Occlusal length M^1–M^3	–	*c.* 71·2	–	–
Occlusal length M_1–M_3	–	75·8	–	–
Occlusal length M_2	–	24·6	–	–
Occlusal length P_2–P_4	–	42·0	–	–

Anteroposterior and mediolateral diameters at the base of other horn cores of *H. gigas* are:

Bed I BM(NH) M 14530	58·0 × 52·1	GHTK II BM(NH) M 29425	62·0 × 55·8
FLK II 068/6663	57·4 × 49·4	Bed II BM(NH) M 21448	84·9 × 72·5
SHK II 1953.281	63·5 × 52·2	Bed II BM(NH) M 21449	74·9 × 62·2
BK II 1963.3042	77·2 × 64·9	F.3014	83·4 × 75·7
BK II East 1953 P.P.R.5	60·0 × 50·3		

The lengths of FLK II 068/6663 and BK II 1963.3042 are 435·0 and 620·0 mm.

Measurements on mandible FLK I G.067/1097 assigned to *H. gigas* are:

Occlusal length M_1–M_3	78·2
Occlusal length M_2	26·0

An immature mandible SHK II 1957.618 has deciduous P_4 measuring 30·1 mm. An immature maxilla DK I 37+43 has deciduous P^2–P^4 measuring 54·9 mm.

Measurements of length and least thickness on the limb bones assigned to *H. gigas* are:

Femur	DK I 3051	288 × 31·2				
Tibiae	FLKNN I 821	321 × 37·8	FLKN I 1450+1459	317 × 33·6	FLKN I 7207	316 × 41·1
Metatarsal	DK I 200	238 × 26·6				
Metacarpals	FLKNN I 826	236 × 24·3	FLKNN I 960	220 × 26·6	FLKN I 5152	250 × 28·9

Measurements of length and least thickness of the limb bones from the tripartite level of FLKNN I are:

Humerus	800M	243 × 30·7	Tibia	800	305 × 35·2
Radius	800D	*c.* 262 × 34·5	Femur	800A	*c.* 296 × 32·0

COMPARISONS. *Hippotragus gigas* is known at Kanjera by paired horn cores BM(NH) M 15853. An unregistered back of a cranium is probably the same individual, since the register describes M 15853 as 'partial skull and horn cores'. The cranium has a very sloping braincase roof, and a short basioccipital with localized anterior tuberosities situated close together. The proportions of the occipital surface and the degree of development of the temporal lines agree with Olduvai

H. gigas. The anteroposterior and mediolateral diameters at the base of the left horn core are 71·0 × 65·6 mm. A rather small frontlet M 15854 (= *H. equinus* of Hopwood *in* Kent 1942 : 126) and part of a horn core M 25721 could also belong to a *Hippotragus* species. There are three fairly large *Hippotragus* teeth from Kanjera. A left upper molar M 25711 and right upper molar M 25695 are more advanced than any Olduvai *H. gigas*, in their larger basal pillars, complicated central cavities, and ribs localized between the styles. Another right upper molar M 25702 is fairly unworn but probably also advanced in its occlusal pattern. These teeth could well be referred to *H. equinus*.

Two *H. gigas* horn cores come from Peninj, A67.230.1 and A67.230.2 (WN 64.178), and are probably from the same individual. The diameters at the base of A67.230.2, the left one, are 71·9 × 62·2 mm.

The base of a right horn core, Omo 29 69-2646 from member G of the Shungura Formation, Omo, is of *Hippotragus* and has basal diameters of 47·4 × 40·2 mm. Part of a right upper molar, L.17-30a from member C, and perhaps a right lower molar, L.7-g129g from member G, are also hippotragine. The occlusal length of the latter is 24·3 and it is in middle wear. These Omo specimens are probably *H. gigas* or an ancestral species.

What is presumably *H. gigas* is known from the Chiwondo Beds of Mwenirondo, Malawi, by a broken right mandible with part of P_4, M_1, M_2 and part of M_3, BM(NH) M 25305. The occlusal length of M_2 is 29·9 mm. It was recorded as hippotragine by Coryndon (1966 : 66).

There is much well-preserved material from Elandsfontein, including the crania 835, 3211, 15819 and 20975, frontlet 8459, and right horn cores 1919 and 9382E, of a large hippotragine which is apparently conspecific with *H. gigas*. Several hippotragine mandibles (right 1569, 6178, 6179, 15834 and 837B; left 1548, 1634, 2349, 6189, 8362, 8641, 20698, 20983 and others; possibly right 20661 and left 20737) are large and presumably *H. gigas*. They have a larger and longer dentition than the roan, but the premolar rows are actually shorter. The Elandsfontein *H. gigas* horn cores are less compressed and smaller than the largest at Olduvai, though the tooth rows are larger than those from Bed I at Olduvai. The temporal ridges are better developed, the braincase shorter, the occipital low and relatively wider and the median vertical ridge and its flanking hollows possibly stronger in Elandsfontein examples than those at Olduvai. It is possible that *H. gigas* grew to a large size in east Africa in Olduvai upper Bed II times and then declined again later. It would also be possible to regard the Elandsfontein fossils as a separate species, but this has not been done here.

H. gigas is also known from Makapansgat Limeworks, being represented by a right lower molar BPI M.8 and two left upper molars M.34 which were assigned by Wells & Cooke (1956 : 23) to cf. *Oryx gazella*. Parts of horn core bases M.1029 and M.1775, both left, and a damaged frontlet with part of the left horn core M.2795, could be this species.

At Florisbad two right lower molars C.1473 with occlusal lengths of 27·9 and 26·5 mm are within the range for *H. gigas* M_2s based on nineteen Elandsfontein specimens (24·6–32·7 mm). This would be a late record for the species, if confirmed.

Hippotragoides broomi Cooke (1947 : 228, fig. 2) is a hippotragine left mandible from the upper quarry at Sterkfontein (Transvaal Museum No. 835). Apart from the extra basal pillars on the medial side of the molar teeth, which are probably an individual anomaly, the dentition appears from the illustration to agree with *Hippotragus*. It lacks characters of *H. gigas*, and agrees so well with *Hippotragus equinus* that it can be taken as conspecific with the latter. Hopwood & Hollyfield (1954 : 164) included *Hippotragoides* in *Hippotragus*, and Mohr (1967 : 66) thought that *Hippotragoides broomi* was inseparable from *Hippotragus equinus*.

A smaller *Hippotragus* which is very probably the recently extinct *leucophaeus* is known from a number of sites in southern South Africa. The species is represented at Elandsfontein by the basal half of a left horn core SAM 848 and an unnumbered complete right horn core, a left maxilla 2824 + 2826, right mandibles 2833, 3319 and 6323, immature right mandible 1546, left mandible 8261, and some single teeth, at Swartklip by mandibles (Hendey & Hendey 1968 : 54; pl. 5A and B), at Eyre's Cave by a left mandible Q644, at Hawston by a left mandible Q131A and at Bloembos by paired mandibles 661A and B which were called *H. problematicus* by Cooke (1947 : 226, fig. 1). Wells (1967 : 100) has previously suggested that *H. problematicus* is identical with *H. leucophaeus*[2]. Klein (1974a) has established the coexistence of *H. leucophaeus* and *H. equinus* at some Cape Province archaeological sites. This shows that the former was not simply a southern subspecies of the roan, as has been maintained by some zoologists (see Mohr 1967 : 20 for details). *H. leucophaeus* is not known from east Africa.

A *Hippotragus* is represented at Broken Hill, Zambia, by the base of a right horn core BM(NH) M 29484. This is probably the horn core which Leakey (*in* Clark 1959 : 230) identified as *Oryx* sp.

Coppens (1971 : 53) has referred to a *Hippotragus* at Garaet Ichkeul, Tunisia, and Bel Hacel, Algeria, both sites of Villafranchian-equivalent age, but the details are to be published later.

The right horn core but not the teeth of *Praedamalis deturi* Dietrich (1950 : 30; pl. 2, fig. 23) from the Laetolil Beds looks hippotragine. The illustration is an anterior view of what was probably a fairly long horn core when complete. It is nearly straight and shows some compression with anteroposterior and mediolateral basal diameters of 45·5 and 34·1 mm. It is inserted fairly uprightly above the back of the orbit, and the pedicel is hollowed internally. The frontals between the horn core bases are at about the same level as the dorsal parts of the orbital rims. It is interesting that the upright insertion and cross-sectional shape of the horn core resemble *Hippotragus* and its straight course *Oryx*. We shall go on using the generic name *Praedamalis*. Laetolil teeth assigned by Dietrich (1950 : 38, 40; pl. 1, figs 11–12; pl. 3, figs 37–40, 42) to *Aeotragus garussi* and *Hippotragus* sp., and similar teeth in the London and Nairobi collections (Pl. 22, fig. 3), could belong, at first sight, to rather primitive Tragelaphini, Hippotragini or even Boselaphini. The basal pillars and slightly rounded ribs between the styles on the upper molars and the less narrowly pointed lateral lobes and less flattened medial walls of the lower molars could fit primitive tragelaphines. However, the bulbous metaconid of two right P_4s, 1959.456 in Nairobi and M 26777 in London, and possibly the indentations of the central cavities of the upper molars make Hippotragini a more likely identification. We believe that these teeth could be of *Praedamalis deturi*.

A Laetolil horn core from Deturi-Mittellauf was figured as 'Aepycerotinae gen. et sp. indet.' by Dietrich (1950 : 30; pl. 4, fig. 45). It is large and long, only slightly compressed mediolaterally, with transverse ridges, a tendency to flattening of the posterior part of the lateral surface and probably with a posterior keel (damage to the basal part precludes certainty on this). Internal hollowing of the pedicel is unlike that of alcelaphines. Seen anteriorly it has quite a strong basal divergence which lessens distally. This and the very poor backward curvature are not unlike *Beatragus*. The base of a left horn core in Berlin labelled 'cf. *Strepsiceros*, K.L. 2/39' from the Garussi area, and the base of a right labelled 'Tragelaphine, 11/13.1.39' (but given as 11/2.1.39 and 11/12.1.39 on its accompanying card) which definitely has a posterior keel, would both be the same species. The horn core assigned to *Gazella kohllarseni* by Dietrich (1950 : 25; pl. 1, fig. 7) could be a female individual of the same species. We assign all this material to ? Hippotragini sp.

A complete left horn core from Sahabi, Libya, now in Rome, is possibly an early member of the *Hippotragus* lineage. It has preserved part of the orbital rim and frontal. Among its interesting features are strong backward curvature, no flattening of the lateral surface, a small supraorbital pit right at the base of the horn pedicel and incipient frontal sinuses. Its length is 320 mm and its basal index 46·7 × 36·6 mm. The Sahabi fauna has been thought to have an age of about 6 million years (Maglio 1973 : 70).

A fossil hippotragine with a resemblance to *H. gigas* is the holotype cranium of *Sivatragus bohlini* Pilgrim (1939 : 80, text-fig. 6; pl. 2, figs 3–6) from the Pinjor Formation of the Siwaliks. It has a short braincase and a small, short basioccipital with localized anterior tuberosities like *H. gigas*, but it differs in being smaller, having more upright horn core insertions, the braincase little angled on the facial axis and temporal ridges stronger at least immediately behind the horn core bases. These characters are reasonably interpreted as primitive, and the last two would support the idea of a boselaphine ancestry for *Hippotragus*. Other characters shown on the

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[2] Mohr (1967 : 64) stated that *problematicus* agreed well with *equinus*, but also that it differed from *leucophaeus*. This second opinion, based on premolar/molar row proportions, apparently arose from comparison with a skull in the Hunterian Museum of Glasgow University, identified as *H. leucophaeus*. However, Mohr's illustrations suggest that the Glasgow skull could well be a sable, in which case the difference of *problematicus* from *leucophaeus* becomes non-proved.

Siwaliks cranium are the probable internal hollowing of the left horn core pedicel, the braincase widening posteriorly and being low and wide, the occipital surface facing partly laterally as well as directly backwards on each side, the mastoids large, the nuchal crests slightly concave upwards and the auditory bullae probably small. *S. bohlini* can probably be placed in *Hippotragus*. The only other species included in *Sivatragus* is *S. brevicornis* Pilgrim (1939 : 83; pl. 2, figs 7–9) which has still more upright horn core insertions and a more angled braincase. It is possible that it is not hippotragine at all. Pilgrim (1939 : 84–86, text-fig. 7) referred to Tatrot dental remains which are certainly reminiscent of Hippotragini, but it is interesting that on P_4 of the mandible BM(NH) M 15373 there is fusion between the paraconid and metaconid, a feature not found in later, more definite Hippotragini.

Supposed Hippotragini from the Miocene of Samos, Pikermi, Maragha and China are really Caprinae (Gentry 1971), and the tribe is unknown outside Africa, Arabia and India.

The right mandible SAM Mb 1 and deciduous right P_4 Mb 122 from Melkbos recorded as cf. *Hippotragus* sp. (Hendey 1968 : 110) are bovine.

Genus ***ORYX*** Blainville 1816

TYPE SPECIES. *Oryx gazella* (Linnaeus 1758).

Oryx cf. ***gazella*** (Linnaeus 1758)

1965 *Oryx* sp. indet. Leakey: 51; pl. 62.

One or perhaps two horn cores represent an oryx at Olduvai. An almost complete left horn core with part of the frontal and orbital rim, FLK I G.390 (Leakey 1965 : 51; pl. 62), is definitely *Oryx*. It is inserted slightly closer to the orbit than in living species, but whether the inclination was equally low cannot be determined. Its length along the front edge is 375 mm, and the anteroposterior and mediolateral diameters at its base are 49·0 and 43·5 mm.

A second specimen may well be *Oryx* but the identification is not quite certain. This is BM(NH) M 14532, the lower part of a horn core with part of the pedicel, found in Bed I in 1932. The pedicel has been crushed, and we cannot say whether the horn core is from the right or left side. Its anteroposterior and mediolateral basal diameters are 40·0 and 36·5 mm.

COMPARISONS. The right mandible BM(NH) M 25304 and probably the immature right one M 25303 from the Chiwondo Beds of Mwenirondo, Malawi, recorded as hippotragine and possibly *Oryx* by Coryndon (1966 : 66) are in our opinion bovine and probably *Syncerus*.

The two left upper molars from Peninj, A67.290 (WN 64.73 MMGN ? USC) and A67.305 (WN 64.209), formerly identified by Gentry (*in* Isaac 1967 : 252) as possibly *Oryx*, are probably alcelaphine, albeit that the second one has a small basal pillar. Oryx teeth are not very markedly specialized in their occlusal pattern, and are therefore likely to be confused with teeth of other antelopes; identifications of oryxes based on teeth alone should be treated with caution.

A small oryx frontlet, Omo 78 69-2731, comes from near the top of member G in the Shungura Formation, Omo, and differs from living oryxes by the slight mediolateral compression, lack of any hint of backward curvature and the rather upright insertion of its horn cores.

Joleaud (1918 : 90, fig. 1) referred a long thin slightly curved horn core from Mansoura near Constantine, Algeria, to *Oryx leucoryx*, believing this to be the specific name applicable to the living west African *O. dammah*. Mansoura is supposed to be of an age equivalent to the Villafranchian, so the horn core is unlikely to belong to a living species despite being very probably an oryx. Coppens (1971) has also referred to an oryx at the Villafranchian-equivalent sites of Garaet Ichkeul, Tunisia, and Ain Hanech, Algeria, but no details are yet published.

A fossil oryx is known by two reasonably well preserved skulls from the Siwaliks. One in Calcutta is *Antilope sivalensis* Lydekker (1878 : 154; pl. 25, figs 1–2), later referred by Lydekker to *Hippotragus* and by Pilgrim (1939 : 77) to a new genus *Sivoryx*. Pilgrim described a second, immature skull in London, 39558, as *S. cautleyi* and made this species the type of the genus. The skulls are probably conspecific, and both were thought by Pilgrim to be of Pinjor age. This fossil oryx differs from the contemporaneous Siwaliks *Hippotragus* in its more angled braincase, absence of temporal ridges on the cranium roof and more obliquely inserted horn cores. Both skulls show very large shallow preorbital fossae which are absent in living oryxes. The London skull shows clearly that the horn core pedicel is hollowed, and that the teeth have basal pillars. The size of the preorbital fossae and the basal pillars are consistent with descent of oryxes from a boselaphine ancestry.

Tribe **ALCELAPHINI**

The Alcelaphini are medium to large, grazing antelopes with long faces, very hypsodont teeth and short premolar rows. They are the commonest antelopes of Olduvai. The group appears to have been in rapid evolution up to the present time but there is a closely similar morphology in many lineages, presumably arising from their adaptations to broadly the same way of life. The main skull features are: skulls long, females horned except in *Aepyceros*, horn core morphology strikingly diverse, horn cores frequently with transverse ridges but generally without keels, often a postcornual fossa which is sometimes shallow and narrow, frontals raised between the horn core bases. Frontals with extensive internal hollowing and a single large sinus extending into the horn core pedicel, braincase short and becoming strongly bent on the facial axis in later forms, temporal ridges wide apart posteriorly, supraorbital pits small, faces generally long and tooth rows set anteriorly, nasals generally long, narrow and without anterior flanges laterally, ethmoidal fissure absent in adults, preorbital fossae still present and often having an upper rim, zygomatic arch usually deepening anteriorly under the orbits, jugal with two broad lobes anteriorly, premaxillae large and rising with nearly even width to a long contact on the nasals, palatine foramina set widely apart, median indentation at back of palate set forward of lateral ones, occipital surface sometimes facing laterally as well as backwards and often with a prominent median vertical ridge, mastoids large, basioccipital with a central longitudinal groove having its sides formed by ridges behind the anterior tuberosities, anterior tuberosities rather wide, foramina ovalia rather large. Upper tooth arcades curved, cheek teeth very hypsodont and with cement, central cavities becoming complicated, medial lobes of upper molars and lateral lobes of lowers rounded, widely outbowed ribs of uppers greatly marked, lower molars without basal pillars or goat folds, short premolar rows, P_2s and sometimes P^2s reduced or absent, P_4s with small hypoconid and with paraconid and metaconid growing together or fused, and mandibles deep under the tooth rows.

The limb bones of Alcelaphini are more distinctive than those of most other antelopes. They show cursorial characters which generally take the form of specializations to improve articulations in the anteroposterior plane, and to allow for strong ligamentous connections around the articular joints. Gentry (1970a : 277–282) discussed cursorial characters in antelope limb bones.

Alcelaphus buselaphus (Pallas 1766), the widespread species of hartebeest, was originally based on the extinct bubal hartebeest of north Africa, but now includes a great variety of named populations, among them the East African *A. b. jacksoni* and *A. b. cokei* as well as the geographically isolated South African *A. b. caama* and *A. b. selbornei*. Fig. 20 shows the great extent of horn core variability within this one species. A high, narrow skull is characteristic of the species, with the horn cores inserted on a high pedicel behind the orbits (or well above the orbits as the head is held in life) and showing rather abrupt alterations in course. The premolar rows are fairly long for an alcelaphine and P_2 is still present.

Alcelaphus lichtensteini (Peters 1849) occurs in grassland areas within the wooded savannah zone from Tanzania to Rhodesia and southern Mozambique. It differs quite markedly from *A. buselaphus* in its wider skull, horn cores inserted widely apart (but still behind the orbits) and longitudinal raising of the midfrontals suture.

Damaliscus lunatus (Burchell 1832) embraces the central African tsessebe (*D. l. lunatus*) and the more northerly races formerly called *D. korrigum*. Like *Alcelaphus buselaphus* the skull is high and narrow, but in this species the horn cores are inserted above the orbits and not on a pedicel, and have a more even curvature with no abrupt changes in course. The horn cores of the tsessebe *D. l. lunatus* are more divergent basally than are those of other races.

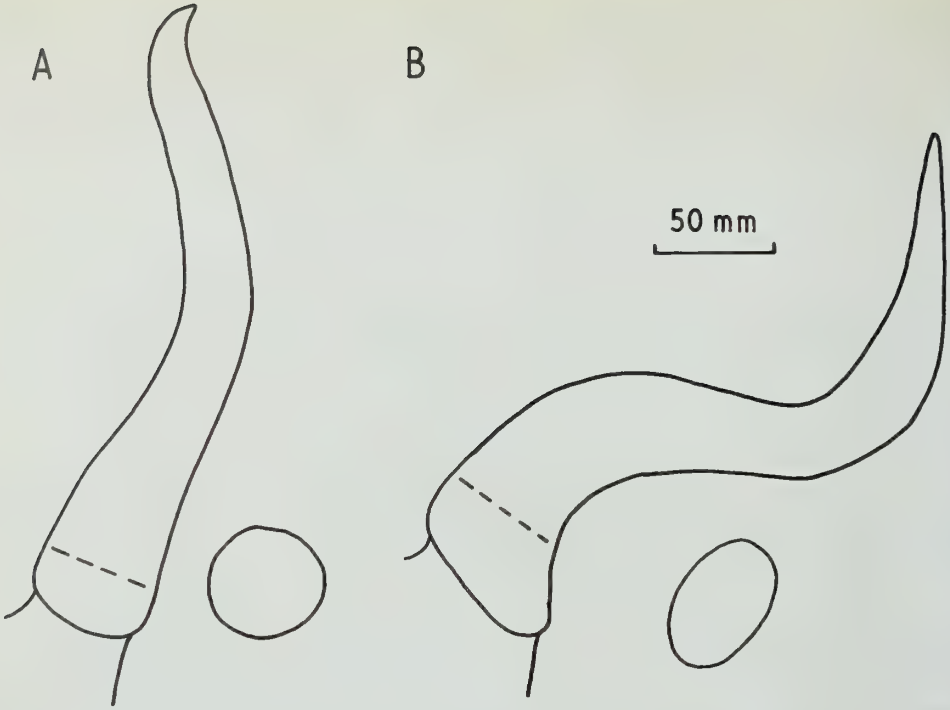

Fig. 20 Infraspecific variation in *Alcelaphus buselaphus* horn cores. A = anterior view and cross-section of left horn core of *A. b. jacksoni*, B = same for *A. b. cokei*. The levels of the cross-sections are marked. The anterior side of the cross-sections is towards the foot of the page.

Damaliscus dorcas (Pallas 1766) is the smaller blesbok and bontebok of South Africa. It differs from *D. lunatus* by having less divergent horn cores, smaller auditory bullae and perhaps more uparched frontals.

Interbreeding between *Alcelaphus* and *Damaliscus* is known to be possible. Selous (1893) referred to a male supposed wild hybrid in Matabeleland (BM(NH) 93.12.17.1). A photograph has been published (*South African Farmer's Weekly*, Bloemfontein, 29 June 1966 : 10) of a hybrid between a male *A. buselaphus selbornei* and a female *D. dorcas phillipsi*. We saw two hybrid skulls (one male, one female) in the Transvaal Museum, Pretoria, apparently the intermediates between *A. buselaphus caama* and *D. dorcas phillipsi* referred to by Kettlitz (1967 : 41). These were such good morphological intermediates that there seems no reason to doubt their origin. Such interbreeding suggests either that the living genera have not been separated for very long or that their gene pools have diverged little since their separation.

Beatragus hunteri (P. L. Sclater 1889), the herola or Tana River hartebeest, has a very restricted range in East Africa. The horn cores are inserted above the orbits and close together, and then diverge outwards. They have long parallel, or sub-parallel, distal parts as in the impala.

Connochaetes gnou (Zimmermann 1780), the black wildebeest of Africa south of the Vaal River, has a wider skull than in *Alcelaphus*, *Damaliscus* or *Beatragus*. The horn cores are inserted well behind the orbits, emerge forwards (downwards with the head vertical), have sharply recurved tips and pronounced basal bosses. The face is shorter than in any other living alcelaphine. The premolar rows are very reduced, and P_2s are missing.

Connochaetes taurinus (Burchell 1823), the blue wildebeest of eastern and southern Africa, has horn cores inserted widely apart and emerging transversely from the skull. The face is longer than in *C. gnou*. This more northern and tropical species is larger than *C. gnou*, just as is *Damaliscus lunatus* in comparison with *D. dorcas*.

C. taurinus has sometimes been generically separated from *C. gnou* as *Gorgon* Gray 1850, and Leakey (1965 : 45) included *Gorgon* in the Bovini. We take *Gorgon* as a synonym of *Connochaetes*, and are happy with the traditional view that it is an alcelaphine (Simpson 1945 : 160; Roberts 1951 : 277; Ellerman, Morrison-Scott & Hayman 1953 : 174). Its skull shows characteristic alcelaphine features: a long face with long narrow nasals, preorbital fossae, the anterior part of the zygomatic arch thickened below the orbits, a bilobed jugal; infraorbital foramen high above the tooth row, a large premaxilla having an even width in side view as it rises to a long contact with the nasals, a central longitudinal groove on the basioccipital and widely set anterior tuberosities, the upper tooth rows well curved with M^3s of opposite sides almost as close as the anterior premolars, very hypsodont cheek teeth, no basal pillars on the molars, rounded medial lobes of upper molars and lateral lobes of lower molars, wide lateral ribs between the styles on the upper molars, lower molars without even incipient goat folds, short premolar rows without P_2s, the P_4 with fusion of paraconid and metaconid giving a continuous medial wall anteriorly, and a deep horizontal ramus of the mandibles.

The limb bones and girdles of *C. taurinus* are very alcelaphine-like in their cursorial proportions and morphology. The *femur* has a fairly deep indentation between the great trochanter and the articular head in anterior view, an anteroposteriorly long lateral part of the articular head and deep pits distally for muscular and ligamentous attachments; the *tibia* has a pronounced tubercle and medial hollow flanking it on the top articular surface, an upcurved edge of the lateral facet and distally a deep central indentation into the rear of the astragalus facet; the *astragalus* has a flange at the top of the medial side visible in anterior view; the *metatarsal* has a greater width across the centre of the top surface than across the rear, lacks a deep hollow between the two naviculocuboid facets and has prominent flanges close together distally on the anterior surface above the condyles; the *scapula* has a large tuber scapulae situated towards the lateral side in ventral view and an unrounded glenoid facet with a posterolateral flattening of its edge; the *humerus* has a wide bicipital groove and a sharp ridge down the front of the lateral tuberosity, a ventral projection at the lateral side of the distal end, distal condyles set uprightly, a small indentation in the top anterior edge of the medial condyle and a well-marked medial groove between the condyles; the *radius* lacks a rim on the medial side of its proximal medial facet, has the back of the lateral facet set well forward of the back of the medial facet, a large and high lateral tubercle, distally the flanges on the anterior surface are strong and close together, and the back of the lunate facet and posteromedial top of the scaphoid facet are well hollowed; and the *metacarpal* has an angled anteromedial corner on its magnum-trapezoid facet and an unciform facet with a small area in relation to that of the magnum-trapezoid facet.

In *C. gnou* some of the alcelaphine-like characters of *C. taurinus* are absent: the long face and nasals, preorbital fossa and anteriorly deepened zygomatic arch. A postcranial skeleton in the South African Museum, Cape Town, failed to show the pronounced tubercle and hollow on top of the tibia, the lack of a deep hollow between the two naviculocuboid facets and the prominent distal flanges on the metatarsal, the small indentation in the medial condyle and the well-marked groove between the condyles of the humerus, and the strong close flanges distally on the radius. Other characters such as the bilobed jugal and the central longitudinal groove on the basioccipital are less pronounced than in *C. taurinus*. However, the unique shape and course of the horn cores of *C. gnou* are not at all like bovines.

Aepyceros melampus (Lichtenstein 1812) is the widespread impala. We classify it as an alcelaphine, but it is undoubtedly well separated from the others.

The Alcelaphini are typically antelopes of open country. Gwynne & Bell (1968 : 390) have shown the connection between the ecological roles of the blue wildebeest and Burchell's zebra on the Serengeti Plains, Tanzania, and a similar relationship could have existed between the black wildebeest and the extinct quagga in South Africa. The extinct north African bubal hartebeest may have lived in rather drier conditions than other hartebeests, perhaps as a result of human persecution. In west Africa *Damaliscus lunatus* ranges further north towards the desert than does *Alcelaphus*, yet in southern Africa *A. buselaphus caama* lives in more arid country than *D. lunatus*.

A number of extinct alcelaphine lineages exist in the fossil faunas, one larger than *Connochaetes taurinus* and at least one smaller than *Damaliscus dorcas*. However, most living and fossil alcelaphines do not differ very much in size. The teeth of Pleistocene fossils show less occlusal complexity, particularly in the folding of the central cavities, than in living species other than perhaps *Connochaetes gnou* and *Damaliscus dorcas*. Because of the rapidity of alcelaphine evolution in the Pleistocene and the late extinction of a number of lineages, it is rather difficult to sort out the stocks.

Genus ***MEGALOTRAGUS*** van Hoepen 1932

1932 *Megalotragus* van Hoepen : 63.
1932 *Pelorocerus* van Hoepen : 65.
1953 *Lunatoceras* Hoffman : 48.
1965 *Xenocephalus* Leakey : 62.

TYPE SPECIES. *Megalotragus priscus* (Broom 1909).

GENERIC DIAGNOSIS. Very large extinct alcelaphines, including the largest known, with narrow skulls and horn cores inserted obliquely in side view, behind the level of the orbits and close together, and with a torsion that is clockwise from the base upwards on the right side; molar teeth tending to have a simple occlusal pattern; very short premolar rows; long legs.

HORIZON. Later levels of the Shungura Formation, Omo, until the end of the Pleistocene.

REMARKS. Our conception is that all the 'giant' alcelaphines of the African Pleistocene can be included in one genus with two species. The species are *Megalotragus priscus*, with long curved horn cores, from South Africa and *Megalotragus kattwinkeli*, an earlier species from east Africa. After Wells (1959 : 124) had considered the species name *priscus* to be a *nomen vanum*, the type cranium of *Bubalis* (= *Alcelaphus*) *priscus* Broom was found in the South African Museum. We were able to see the specimen, SAM 1741, and to confirm its generic attribution to *Megalotragus*. Broom's specific name *priscus* therefore has priority for the South African member of the genus.

Megalotragus kattwinkeli (Schwarz 1932)

1932 *Alcelaphus kattwinkeli* Schwarz : 4, no figure.
1937 *Alcelaphus kattwinkeli* Schwarz : 56; pl. 1, fig. 3.
1965 *Alcelaphus kattwinkeli* Leakey : 60; pl. 78.
1965 *Alcelaphus howardi* Leakey : 60; pl. 79.
1965 *Xenocephalus robustus* Leakey : 62; pls 81–82.
1965 Incertae sedis Leakey: 69 (d) in part.

DIAGNOSIS. Horn cores short to moderately long, inserted behind the orbits but not so far back as to overhang the occipital surface, sometimes dorsoventrally compressed at their bases, with transverse ridges, moderately divergent but much less than in *Connochaetes*, and curved upwards from the base followed by a sharp curve backwards. Median vertical ridge present on occipital, occipital facing primarily backwards and little laterally, basioccipital wide with large anterior tuberosities, auditory bullae small and little inflated.

NEOTYPE. The holotype was a right horn core with frontal, VI-1099 from an unknown horizon at Olduvai, destroyed in Munich in the Second World War. The illustration of this species in Schwarz (1937 : pl. 1, fig. 3) shows a frontal region with horn core bases, which the caption alleges to be VII-468. However, in Schwarz's own list (1937 : 56) of specimens of this species VII-468 is the number of a lower jaw. Further, the skull part shown in pl. 1, fig. 3 does not fit the description of the holotype as a right horn core with frontal. Possibly the figured specimen is in fact VI-487, another listed skull part. Since the original holotype is now lost and was probably never figured, a neotype is now designated: a damaged skull BM(NH) M 21447, previously used and illustrated by Leakey (1965 : 62, pls 81–82) as the holotype of *Xenocephalus robustus* (*International Code of Zoological Nomenclature*, Article 75, Neotypes).

HORIZON. The neotype is from TK (Fish Gully) Beds III–IV at Olduvai, in an area of the Gorge where these beds are not divisible (M. D. Leakey 1971b : 283). It was found in 1931 about 4 feet

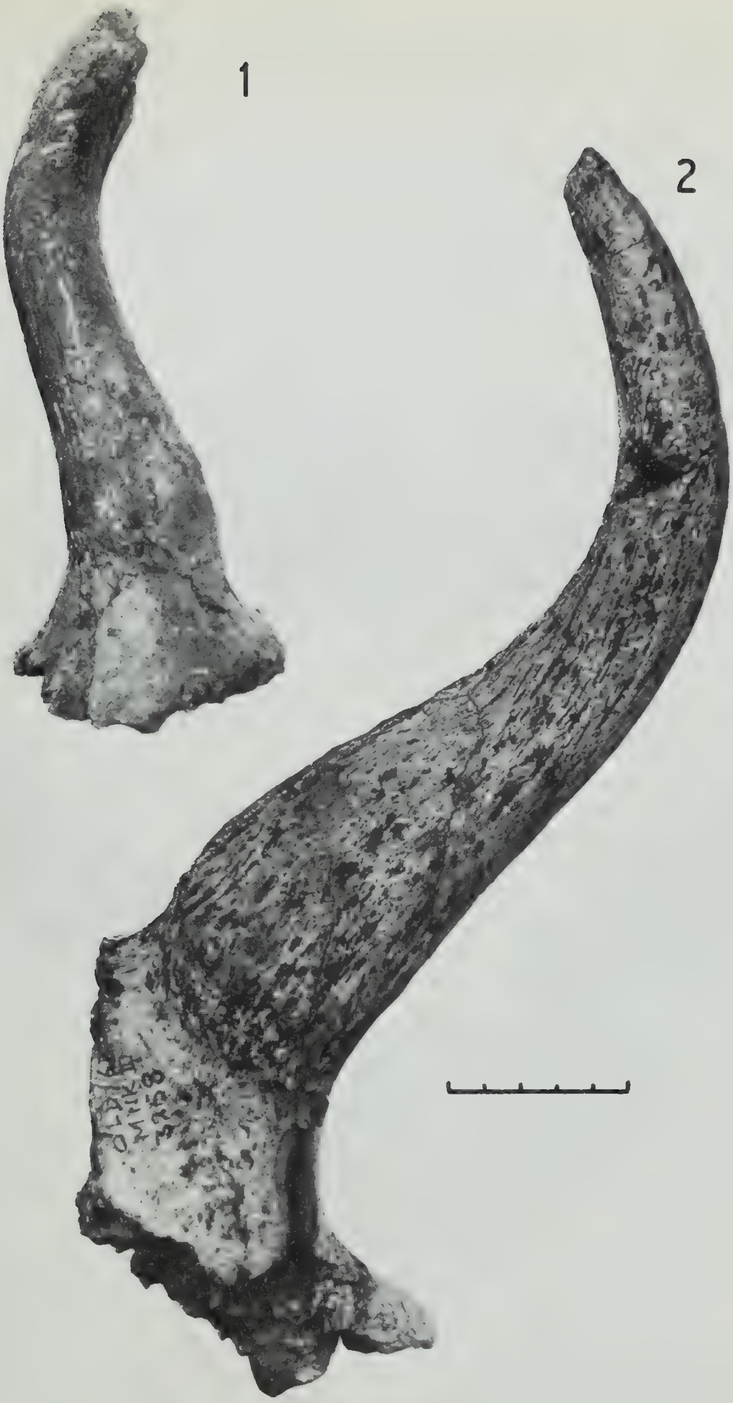

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Plate 12 (Scale = 50 mm)

Fig. 1 ***Beatragus antiquus.*** Anterior view of a female right horn core, HWK East II 131.

Fig. 2 ***Megalotragus kattwinkeli.*** Anterior view of left horn core with orbital rim, MNK II 3258.

(1·2 m) below the Masek Beds. The species is known by frontlets and horn cores from middle Bed II to Bed IV, and by apparently conspecific teeth and limb bones from the base of Bed I upwards. It also occurs at Peninj, Chesowanja, the later levels of the Shungura Formation at Omo and possibly in the 'young Pleistocene' of the Laetolil area.

REMARKS. It is not always easy to distinguish isolated horn cores of *Megalotragus kattwinkeli* from *Connochaetes* unless there are cohering parts of the frontals. However, the large size, narrow skull and very long limbs must have contributed to a very different appearance in life from *Connochaetes*, and, with the tendency to an unadvanced occlusal pattern of the molars, must indicate differences in ecology and adaptations.

The neotype skull is rather poorly preserved, and the nasals, premaxillae and right orbital region are missing. Only the left horn core is present, and it shows the characters of dorsoventral flattening at the base and transverse ribbing. There is no sign of a postcornual fossa. The mid-frontals suture is complicated, but the frontoparietal suture is not visible. The small supraorbital pits lie behind the level of the orbits, and the infraorbital foramina are above the front edge of P^4. The molars are large with a simple occlusal pattern. The premolar row was probably extremely short as it seems there is room only for the P^4 in front of the M^1–M^3; such a condition may be unique and is certainly unknown in any living alcelaphine. This skull provides a definite horn core–tooth association for the species.

Compared with living *Connochaetes taurinus*, the neotype skull is high rather than low and wide, the braincase is longer, the horn cores are inserted close together and less far behind the orbits, and their course lies more backwards than outwards (i.e. less divergent) and not at all downwards. There is much less of a temporal fossa at the side of the braincase; this is linked no doubt with the closer horn core insertions and with their less extremely posterior position. Compared with a fossil *Connochaetes* cranium and horn cores FLKN I 7154, the neotype is again high rather than low and wide in general shape, the horn cores inserted closer together and their divergence less. There is no doubt that the FLKN I fossil is an early form of wildebeest while, as Leakey (1965 : 62) has pointed out, *M. kattwinkeli* is another line. The horn core of the neotype agrees with the one in Schwarz's illustration in its insertion being close to the mid-line of the skull and somewhat behind the orbits, its degree of divergence and its transverse ridges.

Other cranial remains of *M. kattwinkeli* from Olduvai are: a complete left horn core with a postcornual fossa, part of the frontal and orbital rim MNK II 3258 (Pl. 12, fig. 2); the base of a left horn core BM(NH) M 21484 from the surface of HEK II in 1935 labelled 'cf. *Strepsiceros olduvensis*'; a complete right horn core BK II 1963.3383; the base of a left horn core with the frontal BK II 1963.459; a complete right and possibly female horn core A.72 from JK2 III in 1961 with the frontal, orbital rim and a series of supraorbital pits, and part of the right side of the braincase A.78 preserved separated from the horn core; the basal half of a left horn core with the frontal A.2426 from JK2 III in 1962; the base of a right horn core with the frontal 596 from GC IV referred to by Leakey (1965 : 69) as an unusual member of the Caprinae; a probably female frontlet 068/6664 with complete right horn core and most of the left found *in situ* at GTC IV in 1962 (Pl. 13, fig. 1); and a frontlet with incomplete horn cores F.3013 P.P.F.6 referred to *Alcelaphus* cf. *kattwinkeli*, which was a surface find in 1941 (Leakey 1965 : 60; pl. 78) and has a postcornual fossa and a pit representing the top one of a probable series of supraorbital pits on the left side.

The holotype of *Alcelaphus howardi*, a frontlet with complete left horn core and basal half of the right BM(NH) M 14950 from the surface of SC II in upper Bed II (Leakey 1965 : 60; pl. 79), has horn cores less dorsoventrally compressed at their base than in the neotype but very similar to the slight compression of MNK II 3258. There is no doubt of its identity as *M. kattwinkeli*. The size is right and the horn core about the usual length. The horn cores show transverse ridges in the middle section of the dorsal surface and have moderately strong divergence; above their basal parts they begin to rise and turn inwards and nearer their tips they turn backwards, all as in *M. kattwinkeli*. The left and right sides of the frontlet have been stuck together along their mid-line, but it is clear that the horn core insertions were close together. The dorsal surface at the base shows rather a broken spongy texture. The base of a right horn core BK II 1963.2718 labelled *Alcelaphus howardi* differs very little from MNK II 3258.

It therefore appears that only one species of large extinct alcelaphine can be identified at Olduvai, and that the correct name for it is *M. kattwinkeli* (Schwarz). There is no reason to place it in a separate genus from the South African species which differs mainly in horn core characters, and in any case *Xenocephalus* is unavailable, being preoccupied by a fish (Kaup 1858) and a beetle (Wasmann 1887); the beetle was later renamed *Wasmannotherium* by Bernhauer (1921).

As Leakey (1965: 60, 63) has noted, *M. kattwinkeli* has certain resemblances to the living *Alcelaphus lichtensteini*. However, the latter has shorter horn cores with insertions wider apart, a temporal fossa, and a longitudinal swelling in the centre of the frontals between the orbits and the horn core bases. The similarities between them are merely fortuitous.

The simple occlusal surfaces of the molars in *Megalotragus* (Pl. 13, fig. 2; Pl. 36, figs 1, 4, 5) show that the influence of allometry is not paramount in alcelaphine teeth. Extant *Alcelaphus*

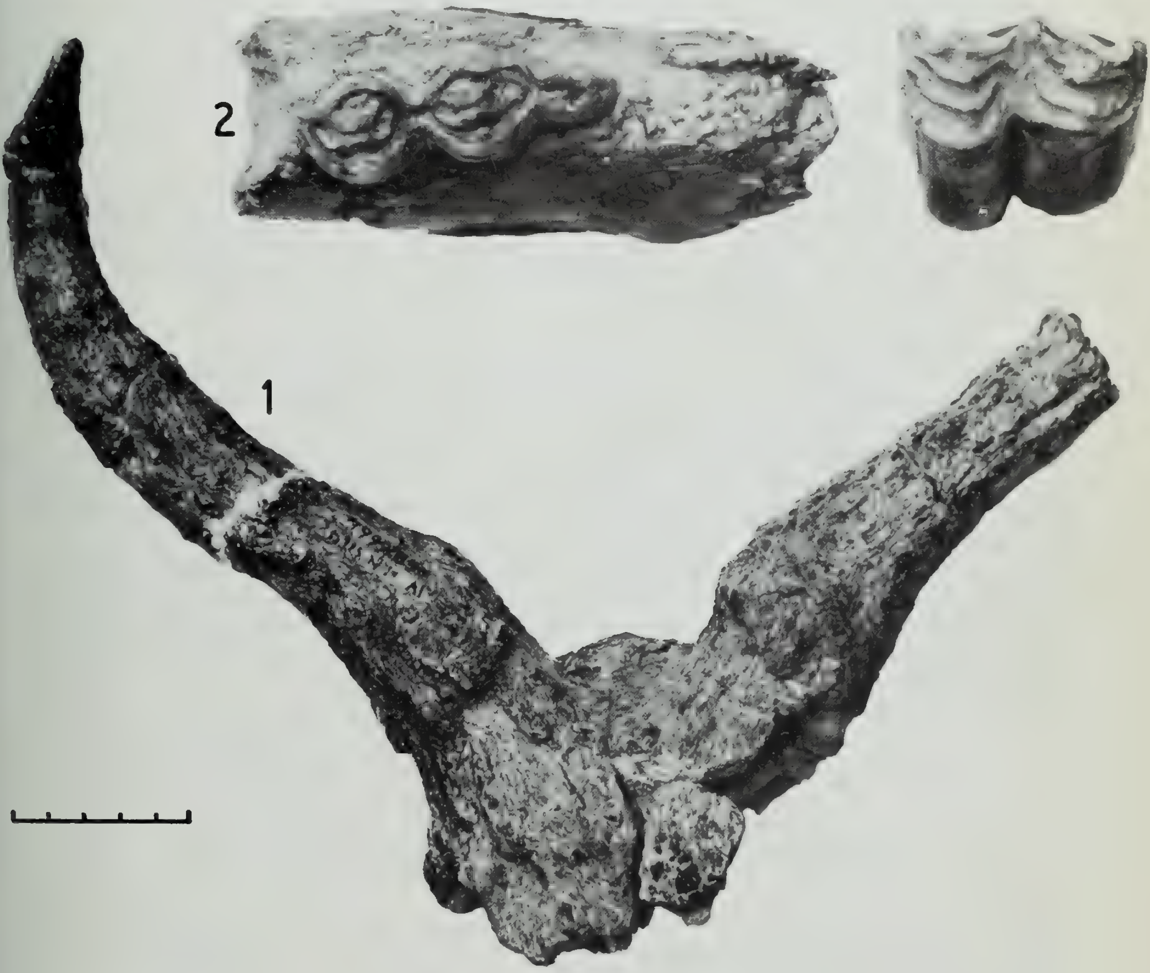

Plate 13 (Scale = 50 mm for the frontlet and 25 mm for the teeth)

Fig. 1 ***Megalotragus kattwinkeli.*** Anterior view of frontlet, GTC IV 1962.068/6664.

Fig. 2 ***Megalotragus* ? *kattwinkeli.*** Occlusal views of teeth: left M_3 DK I 161 (left) and left upper molar DK I 067/3430 (right).

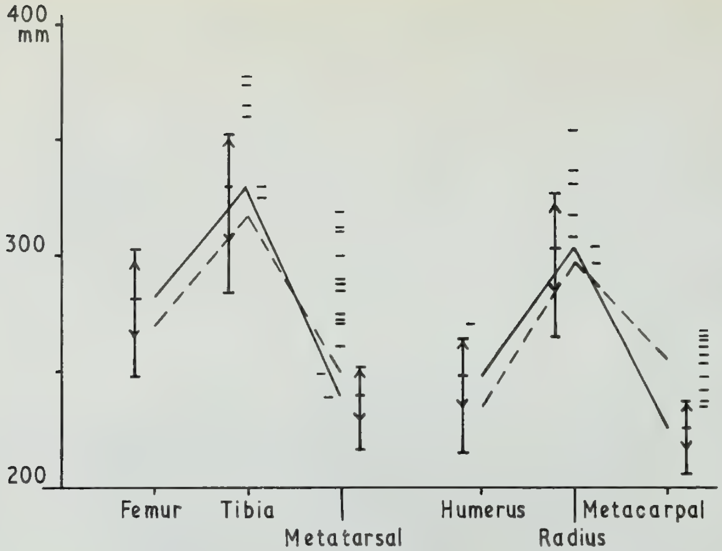

Fig. 21 Lengths of limb bones in *Connochaetes* and *Megalotragus*. Means, ranges and standard deviations are shown for 15 living *C. taurinus*, and the means have been joined up. The dashed line connects the means for *Alcelaphus buselaphus* as a comparison. The metapodials of *C. taurinus* have small ranges and standard deviations. Olduvai fossils are shown as horizontal dashes, the very long bones being of *Megalotragus*.

has fairly complicated occlusal surfaces, and in the larger *Connochaetes taurinus* they are still more complicated, but the very large *Megalotragus* reverses the trend.

Many of the largest alcelaphine limb bones found at Olduvai are too long to fit *Connochaetes* and they almost certainly belong to *Megalotragus* (Fig. 21; Pl. 14). The metacarpal and metatarsal described by Schwarz (1937 : 60, unfigured) as longer than those of *Connochaetes* and assigned by him to *M. kattwinkeli* may have belonged to the latter species, but this is uncertain in the absence of published measurements. However, the left metatarsal VIII-772 assigned by Schwarz (1932 : 4, unfigured) to *M. kattwinkeli* is definitely not long enough for this species, and the radius VIII-345 (Schwarz 1937 : pl. 3, fig. 19) given as *M. kattwinkeli* in the caption but not mentioned in the text is much too small. These limb bones were formerly in Munich but were destroyed in the Second World War.

MEASUREMENTS. Measurements on the more complete specimens of *M. kattwinkeli* are:

	MNK II 3258	JK2 III A.72	TK III–IV M.21447	1941 P.P.F.6 F.3013
Length of horn core along its front edge	280·0	255·0	385·0	–
Anteroposterior diameter of horn core at its base	66·7	48·9	81·9	57·4
Mediolateral diameter of horn core at its base	67·0	48·7	51·5	69·5
Minimum width across lateral surfaces of horn core pedicels	*c.* 130·0	–	129·3	129·6
Width across lateral edges of supraorbital pits	–	*c.* 65·6	*c.* 82·5	–
Maximum braincase width	–	–	107·0	–
Skull width at mastoids immediately behind external auditory meati	–	–	*c.* 175·0	–
Occipital height from top of foramen magnum to top of occipital crest	–	–	67·0	–
Occlusal length M^1–M^3	–	–	92·1	–
Occlusal length M^2	–	–	31·6	–

Anteroposterior and mediolateral diameters at the base of other horn cores of *M. kattwinkeli* are:

SC II surface BM(NH) M 14950	78·1 × 66·8	JK2 III A.2426	54·4 × 49·3
BK II 1963.2718	57·4 × 82·6	GTC IV 068/6664	47·6 × 50·6
BK II 1963.3383	61·3 × 67·3		

The lengths of BK II 1963.3383 and GTC IV 068/6664 are 380·0 and 240·0 mm.

Lengths and least thicknesses of alcelaphine limb bones from Bed I and lower Bed II which could be *Megalotragus kattwinkeli* or its ancestor are as follows. Limb bones and teeth from middle Bed II onwards belonging to size group (i) (see pp. 420–1) include many which are likely to be of *M. kattwinkeli.*

Tibiae	DK I 4300	365 × 35·9	FLKNN I 355	*c.* 377 × 32·0
Metatarsals	DK I 4097	264 × –	HWK East II 2053	319 × 26·4
	DK I 4138	275 × 19·6	HWK East II 067/4691	285 × 24·7
Radii	DK I 166	354 × 37·1	HWK East II 3886	331 × 37·7

Some bones from FLKNN I may be *Megalotragus*, *Connochaetes* or even *Beatragus*. In the account of the FLKNN site we have called them ? *Connochaetes* sp. Their measurements are:

Humerus	358	271 × 34·8	Metacarpal	405	254 × 26·2
Radius	578	304 × *c.* 37·0	Metacarpal	305	235 × 24·1
Metacarpal	577	261 × 27·1			

Radius 578 and metacarpal 577 are associated.

Two large alcelaphine limb bones from FLKN I are:

Metatarsal	8127	312 × 25·2	Radius	181 + 926	297 × 31·0

COMPARISONS. Two Laetolil right upper molars in Berlin referred to *Connochaetes taurinus major* have occlusal lengths of 30·9 (Dietrich 1950 : pl. 2, fig. 18) and 34·6 (pl. 2, figs 19, 20) and therefore are large enough for *Megalotragus*. They come from the 'young Pleistocene' of the Garussi area, not from the old fauna.

M. kattwinkeli is represented at Peninj by left horn core bases A67.228 (WN64.299.2PT3.USC) and A67.234 (WN64.18.CFG III.MZ) and a complete right radius A67.323.1 + A67.345 (WN64. 300A.2PT3.USC). The second horn core was misidentified as *Connochaetes* by Gentry (*in* Isaac 1967 : 253).

M. kattwinkeli is present at Chesowanja in the Baringo district of Kenya (Carney *et al.* 1971 : 509). A young adult right mandible KNM CE 006a + b with P_4–M_3 preserved has occlusal lengths of M_1–M_3 86·7, M_2 29·4 and P_4 17·2. Some single teeth may also be this species.

M. ? *kattwinkeli* is represented in higher levels of the Shungura Formation, Omo by a frontlet with horn core bases F.203-33 and a right horn core F.203-34, both in member K, and by a pair of sub-adult horn cores P.947-1 in member G. These horn cores seem to be 30% or more longer than Olduvai examples, and have a trace of backward curvature at the base. Dorsoventral flattening at the base is poor or absent, and the member G pair are less curved towards the tip. Some of the large alcelaphine teeth in this formation are also likely to be the *Megalotragus* lineage, going back to earlier members.

The large extinct South African *Megalotragus priscus* (Broom) includes *Bubalis helmei* Lyle (1931 : 38), *Megalotragus eucornutus* van Hoepen (1932 : 63), *Pelorocerus helmei* (Lyle) van Hoepen (1932 : 65), *P. mirum* van Hoepen (1947 : 103), *P. elegans* van Hoepen (1947 : 105) and cf. *Megalotragus eucornutus* of Wells (1964a : 88). *P. mirum* and *P. elegans* were placed in a new genus *Lunatoceras* by Hoffman (1953 : 48). Some sinking of names has previously been proposed by Hoffman (1953) and Wells (1959). The species is known by frontlets and horn cores from a good many sites. All the South African specimens are clearly different from *M. kattwinkeli* in their longer horn cores with fairly even curvature, and in the horn core insertions overhanging the occipital surface. They much resemble the horn cores of the bovine *Pelorovis oldowayensis*, but do not reach the size of the largest *P. oldowayensis* and have a stronger upward component of the horn core curvature.

The holotype cranium SAM 1741 of *Megalotragus priscus* (Broom 1909 : 280, 1 text-fig.) comes from the Modder River in the Orange Free State. It is large, and high and narrow rather than low and wide. The remaining base of the left horn core is dorsoventrally very compressed, and the horn cores would have been more divergent than in *M. kattwinkeli*, inserted close together, well behind the orbits and extremely obliquely. The back of the horn core insertions passes above and behind the top of the occipital. The side of the braincase is possibly not hollowed enough to have formed a temporal fossa. The occipital surface is in one plane, facing backwards. There is a median vertical occipital ridge as in *M. kattwinkeli* but it is poorly developed and there are no hollows on either side. The nuchal crests are not very prominent, unlike *M. kattwinkeli*. The basioccipital is wide and has a central longitudinal groove and the anterior tuberosities are probably as wide as the posterior ones.

A good deal of variation occurs in the horn cores of *M. priscus*, notably in the degree of basal divergence. This is weak in specimens from Cornelia, Elandsfontein, Steynspruit and Mahemspan, but strong in those from Florisbad, Mockesdam and Kranskraal and in the holotype cranium. There is a tendency to a flattened medial surface basally in some Elandsfontein horn cores (845 and 851), presumably linked with their poor divergence. The same phenomenon can be seen in some *Alcelaphus buselaphus caama*. It may be that specimens with weak divergence are ontogenetically younger than the others. It may also be true that those with stronger divergence are from later sites, although this conclusion appears to be contradicted by the Mahemspan site. If an evolutionary trend could be detected despite possible ontogenetic effects, then different subspecific names might be justified: *M. p. priscus* (Broom) for those with strongly divergent horn cores and *M. p. eucornutus* van Hoepen for those with little divergence.

It seems to us that none of the South African specimens can be referred to *Alcelaphus* (cf. Wells 1959). The horn cores of '*Pelorocerus helmei*' from Florisbad happen to resemble a huge kongoni hartebeest (*A. buselaphus cokei*) in front view, but in side view (Hoffman 1953 : pl. 1) are considerably different.

The South African *Megalotragus* appears to be later and more advanced than the East African species. It seems unlikely that *M. kattwinkeli*, with its fairly abrupt changes in horn core course and a possible trend towards shortened horn cores, would give rise to *M. priscus*. However, with the evidence of horn core variability in living *A. buselaphus*, there is a possibility that the Olduvai horn cores are a local variation within one widespread and evolving lineage. The horn core insertions of *M. kattwinkeli* are in a primitive, more anterior position than in *M. priscus*, which would be quite compatible with being ancestral to the later species.

There is no clear association of dentitions with *M. priscus*, but many large alcelaphine teeth at South African fossil sites probably belong to this species, as Wells (1964b : 91) has already suggested for the Cornelia and Vaal River material. The tooth material would include the left mandibles C.1584, C.2325 and C.2451 from Mahemspan (Hoffman 1953 : 48) which are complete enough anteriorly to show that there would not have been a P_2 in life, and C.2472 which almost certainly lacked a P_2 in life. Large teeth from the Vaal River gravels and the Wonderwerk Cave assigned to *Pelorocerus broomi* sp. nov., *P. helmei* and cf. *P. helmei* by Cooke (1949), Cooke (1941 : 305, fig. 2) and Wells (1943 : 267) are probably *M. priscus*. Teeth of cf. *P. helmei* from Chelmer, Rhodesia (Wells & Cooke 1955 : 49), and Makapansgat Limeworks (Wells & Cooke 1956 : 25, fig. 12) cannot be safely assigned at species level within *Megalotragus*; this is because teeth from areas to the north of known horn cores of *M. priscus* could be *M. kattwinkeli*, still alive in Olduvai Bed IV times, and because in South Africa no definite horn cores of *M. priscus* are known earlier than Cornelia.

Klein (1972 : 136) has reported teeth from the latest Robberg levels of Nelson Bay Cave, Cape Province, which are the latest known occurrence of *Megalotragus*. They date from 15 000 to 14 000 years BP (Klein, personal communication), shortly before the end of the Pleistocene.

Genus *CONNOCHAETES* Lichtenstein 1814

1850 *Gorgon* Gray.
1934 *Pultiphagonides* Hopwood : 549.

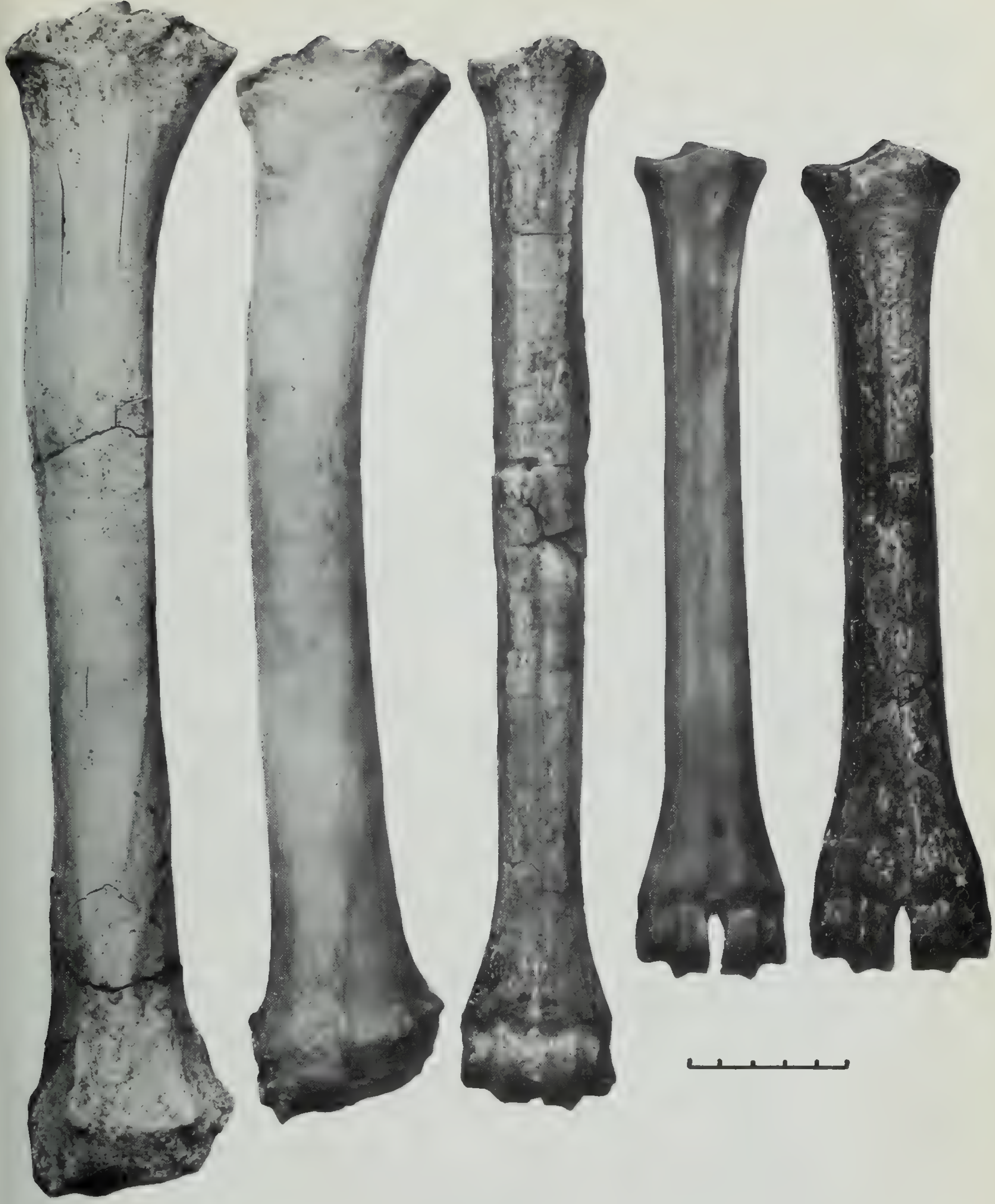

Plate 14 (Scale = 50 mm)

Anterior views of large alcelaphine limb bones. From the left: ***Megalotragus* ? *kattwinkeli***, left radius DK I 166; Recent ***Connochaetes taurinus***, left radius; ***Megalotragus kattwinkeli***, left metatarsal HWK East II 2053; Recent ***Connochaetes taurinus***, left metatarsal; ? ***Connochaetes***, left metatarsal BK II 1953. 067/5509.

TYPE SPECIES. *Connochaetes gnou* (Zimmermann 1780).

GENERIC DIAGNOSIS. Fairly large alcelaphines with skulls tending to be low and wide; horn cores inserted wide apart and behind the orbits, strongly divergent in earlier species and emerging transversely or forwards in later species. Where torsion exists in the horn cores it is clockwise from the base upwards on the right side. Suture of parietofrontals centrally indented behind horn core insertions; preorbital fossae shallow or absent and without an upper rim; posterior suture of nasals indented centrally; greatest width of nasals usually lying anteriorly; anterior tuberosities of basioccipital more localized than in *Alcelaphus* and *Damaliscus*; auditory bullae large and inflated; occipital surface faces backwards rather than laterally; premolar rows very short with P_2s tending to disappear.

REMARKS. *Connochaetes taurinus* is found as early as middle Bed II at Olduvai, while from Bed I to middle II there existed a more primitive species, here called *Connochaetes* sp. In addition the holotype skull of *Connochaetes africanus* from Bed II appears to belong to the lineage of *C. gnou*.

Connochaetes africanus (Hopwood 1934)

1934 *Pultiphagonides africanus* Hopwood : 549, no figure.
1965 *Pultiphagonides africanus* Hopwood; Leakey : 66; pls 93–94.

DIAGNOSIS. A species of *Connochaetes* in which the horn cores are inserted less posteriorly than in either living species and very widely apart; they pass less downwards and slightly more backwards than in *C. taurinus*. A ridge or traces of one pass across the base of the top surface of the horn core from its anterolateral extremity to its posterior edge. The cranial roof is strongly angled. The face is short and not very deep, the nasals are somewhat widened anteriorly, the zygomatic arch is not thickened anteriorly and a preorbital fossa is absent. A median vertical ridge is still present on the occipital.

HOLOTYPE. Skull with the basal half of the left horn core, right M^1–M^3 and left P^4–M^3, BM(NH) M 14688, found in 1931.

HORIZON. The holotype is from Bed II. We have not assigned any other specimens to this species.

REMARKS. *C. africanus* was not placed in a tribe by Hopwood (1934), but was included in the Caprinae by Hopwood & Hollyfield (1954 : 169), and in the Caprini by Simpson (1945 : 162) and Leakey (1965 : 66). However, in the supraorbital pits and top of the orbital rim being well forward of the horn core pedicel, basioccipital with a central longitudinal groove, much curved upper tooth arcade, shape of the molars' central cavities, and upper molars with rounded medial lobes and wide lateral ribs between the styles, the holotype is clearly alcelaphine. Wells & Cooke (1956 : 26, 33) have already stated that *C. africanus* is alcelaphine on the basis of its teeth, although Cooke & Coryndon (1970 : 214) reverted to placing it as ? Caprinae.

M 14688 is about the size of *C. gnou* and somewhat smaller than other *Connochaetes* from Olduvai. It is definitely adult by the fairly worn left P^4, but the left horn core is rather small. The specimen is probably a female. It is a low and wide skull, the horn core insertions are wide apart with the pedicel carrying the horn core well clear of the skull, and the horn core is somewhat twisted in an anticlockwise direction so that the upper surface comes to face partly backwards at the distal end. The horn core insertions are not so far back as the top of the occipital. The supraorbital pits are wide apart, there is no ethmoidal fissure or preorbital fossa, and the back of M^3 is under the front edge of the orbit.

Apart from its specialized horn cores *Connochaetes gnou* differs from *C. taurinus* at the present time in its shorter face with associated characters of shorter nasals and tooth row set less anteriorly, its less deep face, the zygomatic arch being not deepened anteriorly below the orbits, a less clear preorbital fossa, less pronounced bilobing of the jugals, premaxilla narrower in side view, median vertical ridge still present on occipital, greater reduction of longitudinal ridges on basioccipital, and smaller mastoids. The profile of the nasals and diastemal portion of the maxilla and premaxilla in the two wildebeests suggests that the face of *C. gnou* is less bent down on the postorbital part of the skull, and this would be linked with the absence of a shallow doming of the frontals above the orbits such as is seen in *C. taurinus*. It is interesting that in all these characters which are visible, the *C. africanus* holotype agrees with *C. gnou*: the short and low face, short and anteriorly widened nasals, a more posterior tooth row, an undeepened zygomatic arch, no doming of the frontals and no preorbital fossae. In addition, the very great width between the horn core bases seems almost to be leaving space available for the later development of the enlarged basal bosses of *C. gnou*. This implies that *C. africanus* is ancestral to *C. gnou*, and that this lineage has sometimes occurred in the past to the north of its present range. It may be noted that in mid-wear the molars of present-day *C. taurinus* show greater occlusal complexity than in *C. gnou* (perhaps an allometric effect), but this need not have occurred very far back in the ancestry of *C. taurinus* and therefore is of no help in deciding the affinities of *C. africanus*.

MEASUREMENTS. Measurements on the skull of *Connochaetes africanus* are:

Width across lateral edges of supraorbital pits	86·7
Height from maxilla edge between P^4 and M^1 to the maxilla–nasal boundary immediately above, at 90° to the tooth row	59·9
Skull width across mastoids immediately behind external auditory meati	135·4
Occlusal length M^1–M^3	63·6
Occlusal length M^2	22·6
Occlusal length P^4	12·0

COMPARISONS. Material from the Kaiso Formation referred by Cooke & Coryndon (1970 : 214) to *Pultiphagonides* cf. *africanus* does not belong to *Connochaetes*; one horn core has already been mentioned under *Kobus sigmoidalis*, M 12583 and 'M 12558' (= M 12588 ? – AWG) appear to be *Menelikia lyrocera*, while M 26624 is probably alcelaphine but of indeterminate genus. However, the horn core M 12584 does belong to *Connochaetes* (see p. 368).

South African fossils of *Connochaetes* from Cornelia, Elandsfontein and Florisbad can be interpreted as ancestral to living *C. gnou*. The Florisbad *C. antiquus* Broom (1913 : 14, fig. 2) differs from extant *C. gnou* by having horn cores which pass less markedly forwards from the base, and tips perhaps less recurved. At the earlier Elandsfontein site an immediate impression is that the *Connochaetes*, for example the cranium with horn cores 10650, belongs to *C. taurinus* (Wells 1967 : 103), but in fact the base of the horn cores is expanded in dorsal view, and rugose bone has begun to spread across the frontals more than in living or fossil *C. taurinus*. This condition would be appropriate in an ancestor of the black wildebeest. It also occurs in three of the four good *Connochaetes* specimens from Cornelia; these are an unnumbered cranium with complete horn cores, a frontlet C.891 with the base of the left and most of the right horn core, and a partial cranium with left horn core C.892. The fourth specimen, cranium C.622, does not show these features and is much more like *C. taurinus*; it is also the holotype of *Gorgon laticornutus* van Hoepen (1932 : 65, fig. 3). Most probably it is a female. Female horn cores of *C. taurinus* are less anteroposteriorly expanded at the base than males, and the same phenomenon in the Cornelia wildebeest would lead to its females resembling *C. taurinus* males. Horn cores of both the Elandsfontein and Cornelia wildebeests do not pass downwards quite so much, nor are the tips so sharply recurved as in living *C. taurinus*. It is unlucky that nothing is known of the face of the Cornelia fossils to establish beyond doubt that they were on the *C. gnou* lineage. The best classification of this group of wildebeest would be:

Connochaetes gnou gnou the living black wildebeest,
C. gnou antiquus the Florisbad form,
C. gnou ? laticornutus at Elandsfontein,
C. ? gnou laticornutus at Cornelia,
C. africanus from Olduvai Bed II.

Connochaetes sp.

A number of wildebeest fossils from Bed I, lower Bed II and lowermost middle Bed II differ from *C. taurinus* by having horn cores inserted less far behind the orbits, bending less strongly downwards above their base and with tips turned upwards but less inwards. There is no reason to doubt that they are ancestral to *C. taurinus*.

A cranium with complete horn cores and a few isolated teeth, FLKN I 1961.7154 (Pl. 15), was provisionally identified as *Gorgon olduvaiensis* by Leakey (1965 : 46 footnote), but is better designated as *Connochaetes* sp. It is about the size of a female *C. taurinus*, and shows the characters mentioned in the last paragraph. In addition a median vertical ridge was probably present on the occipital.

A horn core cast, HWK EE II 2315, kindly sent to us by Mrs M. D. Leakey in 1972, belongs to *Connochaetes* sp. It is a complete, slender right horn core with much of the frontal, probably from a female animal, and excavated from the Sandy Conglomerate in lower middle Bed II (=level 4 of HWK East II). It has only a short transversely-directed middle section which gives it a markedly primitive appearance. There are transverse ridges on its dorsal surface. We distinguish it from *Megalotragus kattwinkeli* by its long, straight terminal portion, the ridge on its posterior edge near the base, and by the great distance of the insertion from the skull's mid-line as indicated by the incipient temporal fossa. If we are correct in postulating widely separated horn core insertions, then the preserved medial edge of the frontal does not lie along the mid-frontals' suture.

The base of a left horn core with part of the frontal and parietal, BM(NH) M 14518 from Bed I, is of *Connochaetes* sp.

Teeth and limb bones of wildebeest-sized alcelaphines occur at several Bed I sites. They include a left maxilla FLK I B.067/1093 with molars differing from those of the common Bed I alcelaphine *Parmularius altidens* in their greater size and more complicated central cavities. It also has less rounded medial lobes, but this could be a feature resulting from being in early wear; the more worn teeth of FLKN I 7154 have rounded medial lobes. A complete right metacarpal FLKN I 5107 is alcelaphine but not identifiable as *P. altidens* since it is shorter and the distal condyles are too low and wide in anterior view. It could well be of a wildebeest. Some limb bones from FLKNN I have been called ? *Connochaetes* sp., but could easily be of *Megalotragus* or some other large alcelaphine.

Measurements. It is difficult to measure anteroposterior and mediolateral diameters at the base of *Connochaetes* horn cores. Those of *Connochaetes* sp. are:

FLKN I 7154 (left)	47·0 × 53·4
HWK EE II 2315 (cast)	46·1 × 54·7
BM(NH) M 14518	56·7 × 58·9

The lengths of the first two are 330·0 and 463·0 mm respectively.

Measurements on dentitions are:

	FLK I B.067/1093 (maxilla)	FLK I B.17 (mandible)	FLKN I 1431 (mandible)
Occlusal length M1–M3	75·5	79·9	76·1
Occlusal length M2	26·7	25·7	23·6

An immature maxilla FLKN I 067/240 has an M^2 measuring 25·8 and deciduous P^2–P^4 at 45·2 mm.

Limb bone measurements of the FLKNN I ? *Connochaetes* sp. have been given on p. 361.

Comparisons. *Antilope tournoueri* Thomas (1884 : 15; pl. 7, fig. 1) was founded on a skull top of a primitive wildebeest from Ain Jourdel near Constantine, Algeria. It is of Villafranchian-equivalent age, but from a lower level than the kudu already mentioned from Ain Jourdel (p. 304). Thomas's illustration is a mirror image of the actual specimen. The horn cores are set widely apart and close behind the orbits, they have a circular cross-section and transverse ridges, they curve gently upwards all the way from the base rather than having the upward curvature more localized towards the tips, they diverge strongly but less than in other living or fossil wildebeests, and there is not a noticeable transverse ridge running across the base of the horn core. The primitive characters of insertions so close to the orbits, the consistent and steady upward curvature and the less extreme divergence suggest that the fossil is of greater antiquity than the Olduvai *Connochaetes* sp. A shallow upward doming of the frontals anterior to the horn bases would link it to the *C. taurinus* rather than to the *C. gnou* lineage. Thomas wrongly

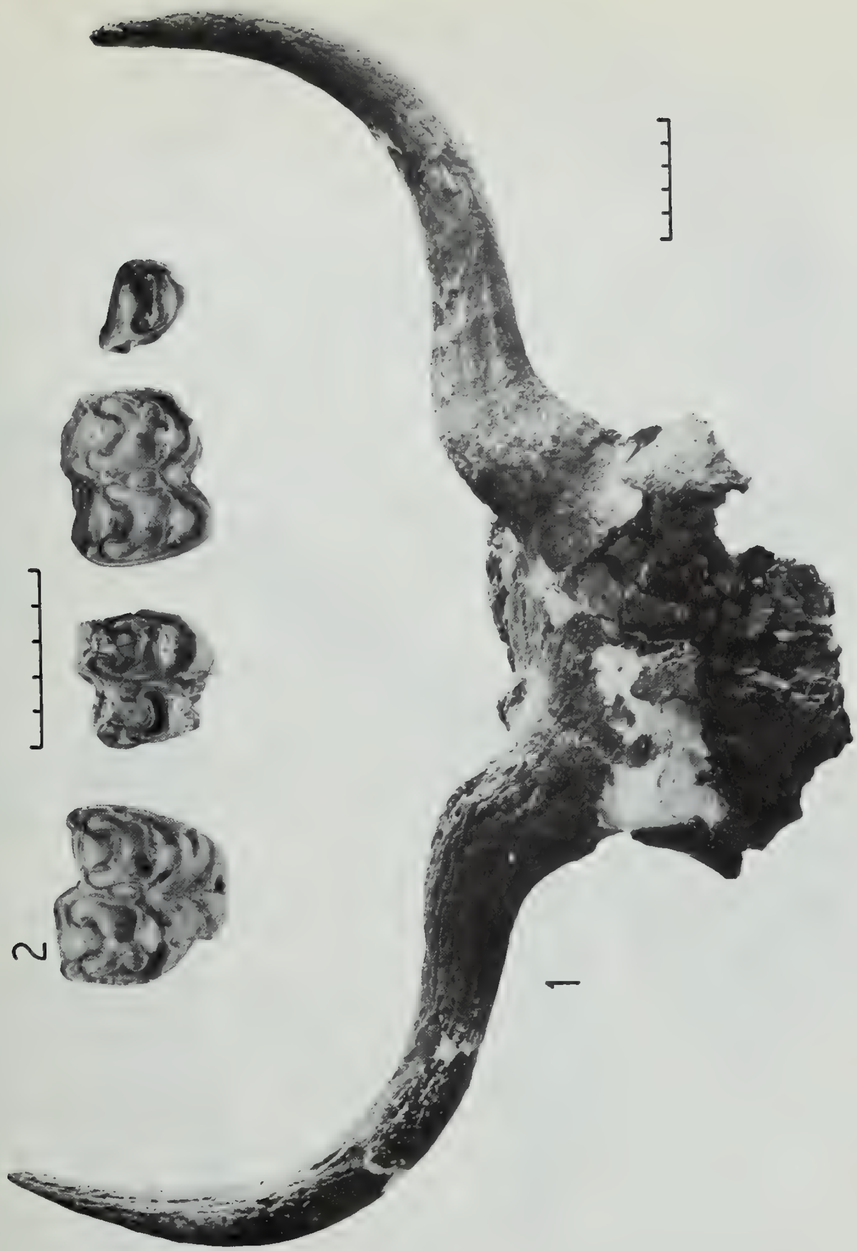

Plate 15 (Scales = 25 mm for teeth and 50 mm for cranium)

Connochaetes sp.; FLKN I 7154

Fig. 1 Anterodorsal view of cranium with horn cores.

Fig. 2 Occlusal views of upper teeth; from the left a right molar, two left molars and a right premolar.

considered that *A. tournoueri* belonged to the Reduncini, and he was followed in this opinion by Pomel (1895 : 45) who founded the generic name *Oreonagor* for it, and by Joleaud (1936 : 1176). Arambourg (1947 : 521) listed it as belonging to *Gorgon*, and the single huge smooth-walled sinus within the right horn pedicel as well as its characters reminiscent of later wildebeest leave no doubt of its alcelaphine status.

The basal half of a right horn core BM(NH) M 12584 from the later faunal assemblage of the Kaiso Formation at Kaiso village belongs to *Connochaetes* or possibly *Oreonagor*[3]. The same identification can probably be made for a horn core L.1-52 from below tuff C of the Shungura Formation.

A complete right horn core, Omo 255 73-5272 from high in member G of the Shungura Formation, belongs to the *Connochaetes* sp. of early Olduvai age rather than to *Oreonagor tournoueri*. It has slight mediolateral compression basally and transverse ridges. Its course is upwards and backwards, then outwards and finally upwards towards the tip.

Connochaetes taurinus (Burchell 1823)

DIAGNOSIS. A larger wildebeest than *C. gnou*; horn cores inserted at the back of the skull above the occipital surface, emerging transversely, having tips turned upwards and inwards, and without a ridge passing across the base of the horn core from its anterolateral extremity; a long face and nasals; zygomatic arch deep anteriorly below the orbits; large shallow preorbital fossa; jugal with two broad anterior lobes; wide premaxillae ascending to a long contact on the nasals; no median vertical ridge on occipital.

Connochaetes taurinus olduvaiensis (L. S. B. Leakey 1965)

1965 *Gorgon olduvaiensis* Leakey : 45; pls 49, 50, 52.

DIAGNOSIS. An extinct subspecies differing from living *C. taurinus* in the horn cores being inserted at a slightly less posterior level and passing less downwards as they emerge from the skull.

HOLOTYPE. Top of a cranium with much of its right horn core and base of the left, BM(NH) M 21451 (Leakey 1965 : pls 49, 50).

HORIZON. The holotype was found at site VEK at the junction of Beds III and IV. It was found in 1932 according to its label or in 1935 according to Leakey (1965 : 45). Other specimens come from Beds II to IV at Olduvai, Laetolil and Peninj.

REMARKS. Other specimens assigned to *C. taurinus olduvaiensis* are a left horn core BK II 1953 P.P.F.1 (Pl. 16, fig. 3; Leakey 1965 : pl. 52 lower picture, which is not BM(NH) M 21452 as stated and is a rear view), and an almost complete right horn core with frontal M 21452 found in Bed IV in 1931 which is the paratype according to the register (Leakey 1965 : pl. 52 top picture which is a dorsal view). A pair of incomplete horn cores 068/6652, together with several pieces of braincase, a right upper molar and an incisor or canine, were found on the surface at MJTK II in 1962 (Leakey 1965 : 105), and may be this subspecies. An incomplete left horn core MNK II

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[3] Since one of us originally informed Cooke & Coryndon (1970 : 214) of the presence of the reduncine *Menelikia lyrocera* in the later fauna at Kaiso, we have looked again for characters whereby its horn cores can be told from those of *Connochaetes*, *Oreonagor* and *Beatragus*.

We found that *Menelikia lyrocera* horn cores from members E and F of the Shungura Formation rise nearly parallel to one another before diverging strongly and bending backwards, hence pieces of sufficient length may show a stronger curve than the alcelaphines. This difference does not exist for many of the *M. lyrocera* from member G and above. Like *Connochaetes* and *Oreonagor* their torsion is clockwise on the right side, so if the side is known *Beatragus* can be eliminated. *Menelikia lyrocera* horn cores taper more rapidly above the base, especially those from member G and above. They have well-marked transverse ridges, which differentiate them from most *Connochaetes*. The sinuses of their frontals rise less far into the horn pedicels and the chambers are smaller than in the alcelaphines.

By these criteria it now appears that the Kaiso horn core BM(NH) M 12584 is of *Connochaetes* or *Oreonagor*. The Kaiso horn cores M 12583, M 12588, M 12589, M 12593 and possibly M 12591 stay as *Menelikia lyrocera*. They resemble horn cores from members E, F and possibly G of the Shungura Formation, Omo, so it is difficult to have them at a time level before member E as suggested by the correlations of Cooke & Coryndon (1970 : 184) and Maglio (1970 : 331; 1973 : 70).

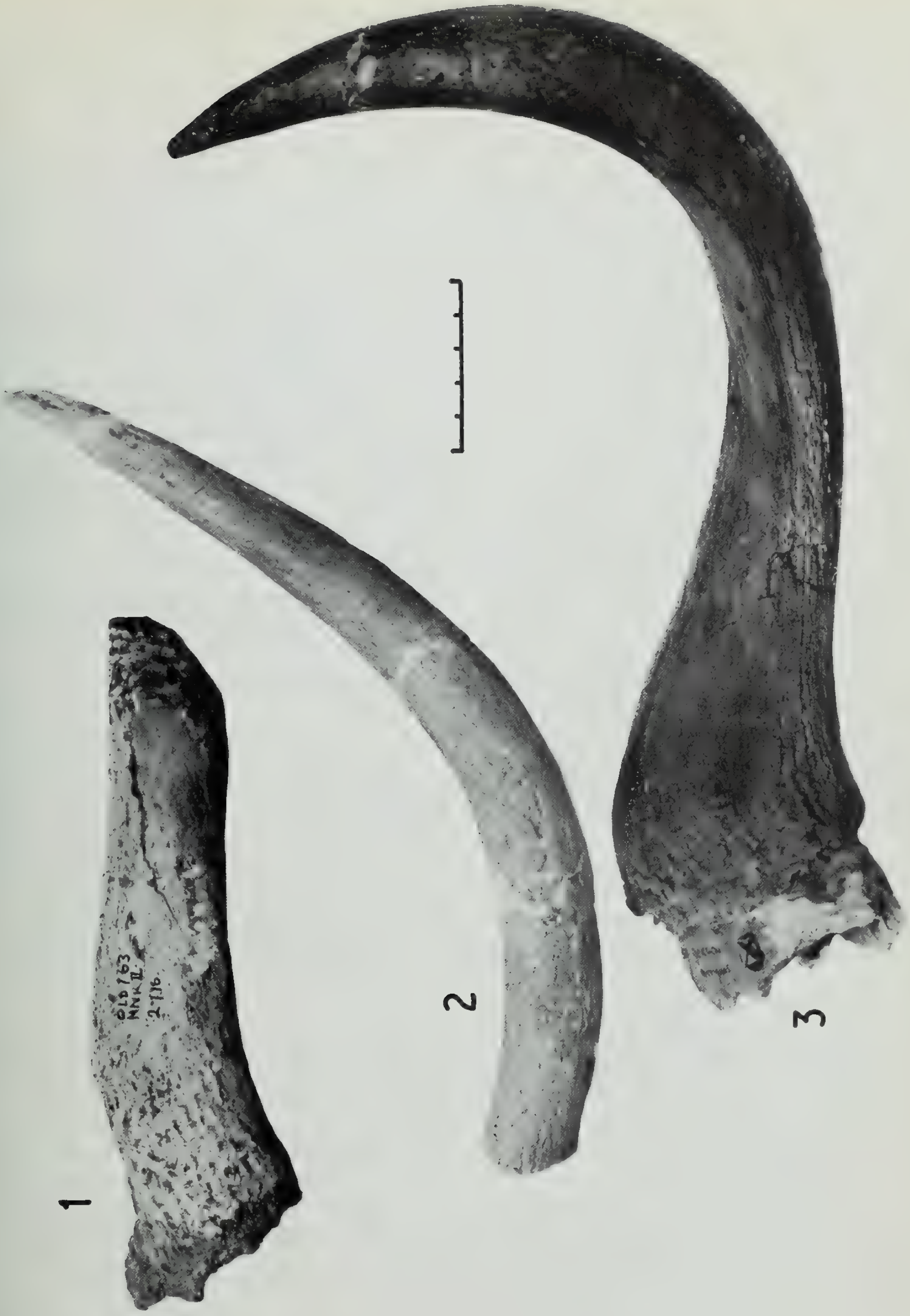


Plate 16 (Scale = 50 mm)

Fig. 1 ***Connochaetes.*** Left horn core, MNK II 2716.

Fig. 2 ***Connochaetes.*** Distal half of a horn core, SHK II 1957.946.

Fig. 3 ***Connochaetes taurinus olduvaiensis.*** Left horn core, BK II 1955 P.P.F.1.

2716 (Pl. 16, fig. 1) is probably a female, and may belong to this subspecies. It would be the earliest Olduvai *C. taurinus*, if it could be definitely distinguished from *Connochaetes* sp. Some other registered pieces in London may belong either to this species, or if the Bed I origin of some of them is to be relied on, to *Connochaetes* sp. These are: M 14522 from Bed I, a tip M 14524 from Bed I, M 14534 from Bed I, M 14548 from Bed II, M 14555 from Bed III, a tip M 14556 from Bed III, M 14559 from Bed III, M 14562 from Bed IV and probably M 14527 from Bed I.

The horn cores of *C. taurinus* no longer show any sign of the ridge passing across the base of the front surface from its anterolateral extremity. The effect is as if the former lateral part of the base had become anterolateral by a twisting of the axis. Such a change would be connected with the increasingly transverse emergence of the horn cores.

Some of the fossils show the beginnings of rugose surfaces over the frontals immediately adjacent to their bases, e.g. BK II 1963.1353. This can also be seen in some living *C. taurinus*. Longer series of complete horn cores might show that the tips were less inwardly recurved in *C. t. olduvaiensis* than in living *C. taurinus*; at present we do not know.

Reck (1935 : 218, fig. 1) described an extremely odd-looking skull fragment from Olduvai as *Rhynotragus semiticus*. It had a strongly-arched or updomed profile of the nasals. Schwarz (1937 : 60, 85) supposed that the fossil had been considerably distorted and was really from a wildebeest. He used the name *semiticus* as a subspecies of *C. taurinus* and assigned a great deal of other Olduvai material collected by Reck to the same subspecies. Assuming that this material was all alcelaphine, we doubt that the dentitions, vertebrae and limb bones could all be safely assigned to *Connochaetes*. (Nine pieces of this Reck collection have survived in London, presumably from a pre-war loan to Schwarz, and all are likely to be alcelaphine, but it is much less certain that they can only represent a wildebeest.) The odd holotype of *R. semiticus* seems unlikely to have been a wildebeest because of the lack of a sharply-outlined temporal fossa between horn core base and orbit and the slope of the braincase just behind the horn core bases.

MEASUREMENTS. Measurements on the holotype cranium BM(NH) M 21451 of *C. t. olduvaiensis* are:

Dorsoventral diameter of horn core at its base	53·9
Anteroposterior diameter of horn core at its base	75·2
Minimum width across lateral surfaces of horn core pedicels	169·0
Length from midfrontal suture at the level of the supraorbital pits to top of occiput	159·0

Anteroposterior and mediolateral diameters at the base of other horn cores of *C. t. olduvaiensis* are:

MJTK II 068/6652	41·4 × 71·8	BK II 1955 P.P.F.1	55·5 × 75·5
MNK II 2716	45·9 × 47·8 (perhaps not this subspecies)	BK II 1963.1353	57·9 × –
		Bed IV BM(NH) M 21452	61·9 × 84·2

The length of BK II 1955 P.P.F.1 is 385·0 mm.

COMPARISONS. Two pieces of one or more right horn cores 1959.44 and 1959.45, and possibly part of a third 1959.337, from Laetolil are of *Connochaetes* and comparable with horn cores from BK II and living *C. taurinus*. They do not derive from the older horizons of Laetolil.

Two pieces of a large skull on which the horn cores have not been preserved, A67.268 (WN64.388 MMG.BSC) from Peninj, belong to *Connochaetes*. The width across the left frontal from the mid-line to the missing horn core base is too great for *Megalotragus*. The anteroposterior level of the horn core insertions agrees well with *C. taurinus olduvaiensis*, the face is longer than in *C. africanus*, and a preorbital fossa of moderate area and extreme shallowness is present. The occipital is rather high, which is probably linked with the anteroposterior level of the horn core insertions. The skull is very large in comparison with the living blue wildebeest. *Connochaetes* is also represented at Peninj by a left horn core base A67.233 (WN64.14 CFG III.MZ), the distal part of a right horn core A67.250 (WN64.142 RDGS.BSC), the middle part of a horn core A67.241 (WN64.238 JHG? USC?), and other horn core, dental and limb bone remains. The distal horn core is about as recurved as in living *C. taurinus*. We identify the Peninj fossils as *C. t. olduvaiensis*.

Arambourg (1938 : 38) assigned a cranium from Témara, Morocco, to *C. taurinus prognu* Pomel, drawing attention to the high occipital and to the short distance between the horn core base and the orbit. His pl. 4, fig. 4 illustrates this last character, and his pl. 3, fig. 3 shows that the horn cores do not pass at all downwards as they emerge from the skull; both these features suggest the strong possibility of subspecific identity between the Moroccan and Olduvai wildebeests. We have not formally sunk *C. t. olduvaiensis* because the original material of *C. t. prognu* described and illustrated by Pomel (1894 : 9; pl. 3, figs 1–4 for horn cores) is insufficient for reliable subspecific determination and because Témara, being of late Pleistocene age, may postdate the east African time range of *C. t. olduvaiensis*. Description of further material of *C. t. prognu* from the type locality (Palikao = Ternifine) may appear in Arambourg's forthcoming monograph. *C. taurinus* survived in north Africa until the late Pleistocene, but Arambourg (1938 : 42) was doubtful about claimed Neolithic occurrences.

C. taurinus is represented at Broken Hill, Zambia, by a number of horn cores, including the left BM(NH) M 12145 and right M 12911 and M 12912. However, some of the horn cores mentioned by Leakey (*in* Clark 1959 : 230) under *Connochaetes* sp. appear to us to be of *Alcelaphus lichtensteini* or its immediate ancestor.

Teeth of *Alcelaphus robustus* from the Vaal River gravels (Cooke 1949 : 20) and of cf. *Alcelaphus robustus* from Makapansgat Limeworks (Wells & Cooke 1956 : 25, fig. 12) may well belong to *Connochaetes*, but of unknown species. The same conclusion should probably also apply to the Chelmer teeth of *Connochaetes grandis* (Cooke & Wells 1951 : 206, fig. 2).

Genus ***PARMULARIUS*** Hopwood 1934

1934 *Parmularius* Hopwood : 550.

Type species. *Parmularius altidens* Hopwood 1934.

Generic diagnosis. Extinct alcelaphines about the size of *Alcelaphus buselaphus*. Horn cores moderate to long, slightly compressed mediolaterally, without keels or torsion, occasionally with transverse ridges in their distal parts, inserted obliquely over the back of or behind the orbits and close together, usually not very divergent but more so distally, and tending to have posteromedial, posterior or posterolateral swellings at the base. Horn core pedicels long (partly connected with the oblique insertions); horns in females; postcornual fossae present; braincase short and strongly angled on the facial axis; a parietal boss placed centrally on the braincase roof; orbital rims moderately projecting; supraorbital pits not set notably wide apart; preorbital fossae small; auditory bullae rather small and not very inflated; premolar rows short; lower molar row sometimes appearing rather small relative to the mandible size.

Horizon. Beds I–IV at Olduvai. Also found at Peninj, Isimila, Kanjera, the later Shungura Formation at Omo, and possibly Laetolil and Elandsfontein.

Remarks. Three species of the genus have been named, all with holotypes from Olduvai Gorge: *Parmularius altidens* Hopwood, *P. angusticornis* (Schwarz) and *P. rugosus* L. S. B. Leakey. *Parmularius* probably derives from the same ancestry as *Damaliscus* and *Alcelaphus*, but became more specialized earlier in time. It is not known to have survived the Pleistocene.

Parmularius altidens Hopwood 1934

1934 *Parmularius altidens* Hopwood : 550, no figure.
1965 *Parmularius altidens* Leakey : 56–59, first, second and third additional specimens; further additional specimens (a), (c), (d) and (e), pls 70–74. The horn core FLK I G.230, referred to as a right horn core of *P. altidens* in (b), is in fact the left one of a pair of *Antidorcas recki* horn cores, but possibly the *P. altidens* right horn core 233 is meant. The horn core of pl. 74 is not FLK I F.206 but FLKN I 1410.
1965 Incertae sedis. Leakey : 68(b).
1965 *Okapia* Leakey : 35.

Diagnosis. A species of *Parmularius* about the size of *Alcelaphus buselaphus* or slightly smaller. Horn cores less massive and less divergent in their distal parts than in *P. angusticornis*; earlier populations probably with horn cores strongly and nearly evenly curved backwards, the backward curvature later becoming more distal and finally almost disappearing; horn cores with localized medial or posteromedial swellings at the base. Braincase shortened and strongly angled on the facial axis; large parietal boss on braincase roof; parietofrontals suture indented in front of the parietal boss; each side of the occipital surface facing partly laterally; auditory bulla perhaps larger than in later *Parmularius* species; central cavities of upper molars not quite so curved as in living *Alcelaphus* and *Damaliscus*; premolar rows short; P_2s sometimes absent.

HOLOTYPE. Skull with the basal part of both horn cores, mandibles and cervical vertebrae, BM(NH) M 14689, found in 1931.

HORIZON. The holotype was found in upper Bed I near the mouth of the HWK gully (M. D. Leakey 1971b: 286; personal communication). Other specimens come from Bed I and from member H of the Shungura Formation, Omo.

REMARKS. *P. altidens* is a common alcelaphine at Olduvai. The holotype skull is about the size of a blesbok and is high and narrow rather than low and wide. The horn cores are mediolaterally compressed and inserted behind the orbits. The postcornual fossae are shallow and elongated. The braincase sides are parallel in dorsal view, and the skull-top sutures are not very complicated. The supraorbital pits lie just behind the plane of the middle of the orbits. The zygomatic bar is probably deepened below the orbit; it survives only on the left side and the surface of the bone has disappeared. The back edge of M^3 lies at a level below the front edge of the left orbit; the right orbit is missing apart from some restoration in plaster. The nuchal crests are not very prominent, and each side of the occipital surface probably faced posterolaterally although the central parts have been plastered. The mastoids are large. A number of characters of the face would probably have been found throughout the genus: the small and very shallow preorbital fossae, slight upper rims to the preorbital fossae, infraorbital foramina above the front halves of the P^4s, and the wide premaxillae. The mandibles are large and deep, and both upper and lower

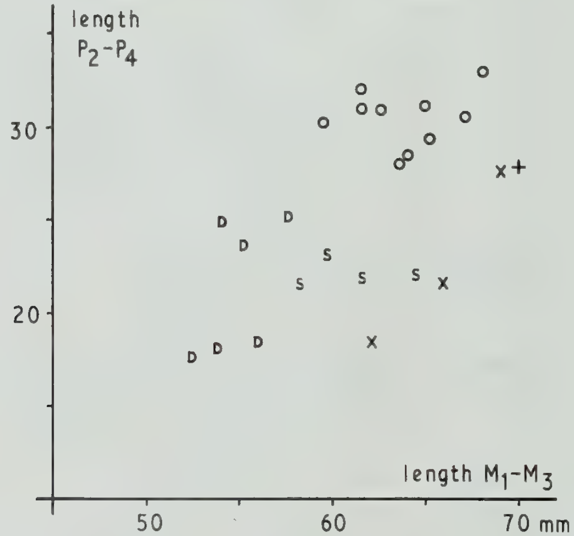
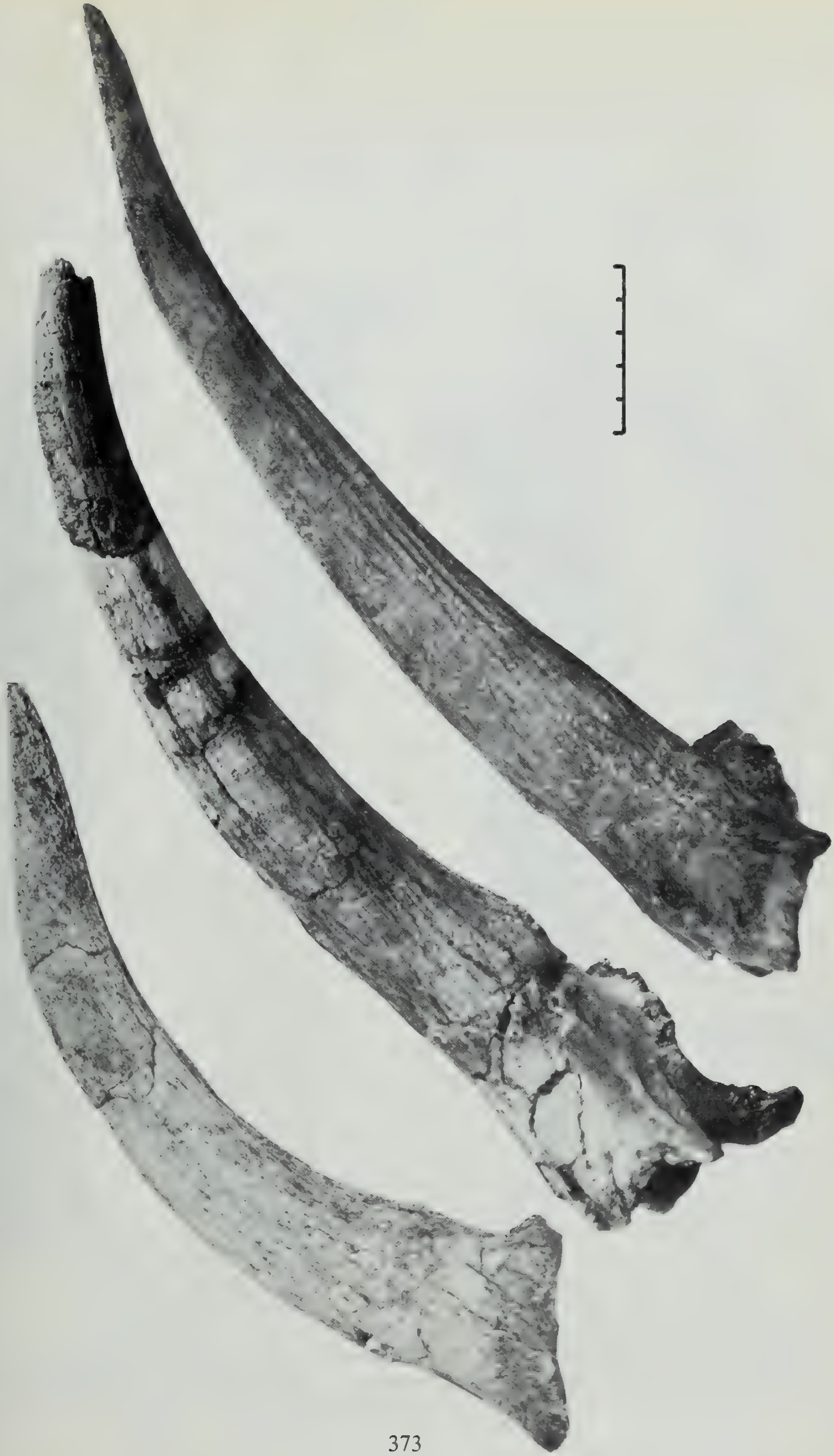


Fig. 22 Lower premolar row/molar row proportions for some alcelaphines. O = East African *Damaliscus lunatus*, D = *D. dorcas*, S = *D. agelaius*, X = *Parmularius altidens*, + = *Damalops palaeindicus* BM(NH) 39571. *Damaliscus agelaius*, having no P_2, has a shorter premolar row than living *Damaliscus* but not as short as the *Parmularius*.

Plate 17 (Scale = 50 mm)

Horn cores of ***Parmularius altidens*** to show the evolution of a straighter profile in Bed I. From the left: medial view of right horn core, DK I 068/6696; lateral view of left horn core of frontlet, FLK I Balk 126+199; lateral view of left horn core, FLKNI 1410 P.P.R.6.



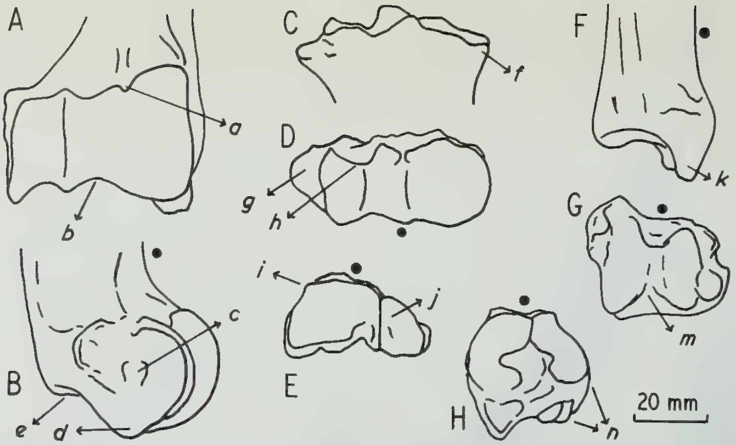


Fig. 23 Limb bones of *Parmularius altidens* from FLKN I to show alcelaphine characters. (Solid dots show anterior sides.)

A. Anterior view of distal right humerus 1961.7070.
B. Lateral view of same distal humerus.
C. Anterior view of proximal right radius 1960.2+57.
D. Proximal articular surface of same right radius.
E. Proximal articular surface of right metacarpal 1962.8836.
F. Medial view of distal left tibia 1961.7074.
G. Distal articular surface of same tibia.
H. Proximal articular surface of right metatarsal 1960.88.

a = indentation at top of medial condyle,
b = deeply incised medial groove,
c = deep hollow for lateral humeroradial ligament,
d = V-shaped ventral edge of lateral side,
e = high level of back part of lateral side distally,
f = no medial rim on top articular surface,
g = large lateral tubercle,
h = back of lateral facet set well forwards,
i = angled magnum-trapezoid facet (less marked than in living alcelaphines),
j = relatively small unciform facet,
k = medial malleolus, less long than in living alcelaphines,
m = deep rear indentation into distal articular surface,
n = articular surface less wide posteriorly than in the centre.

P2s are present. Leakey (1965 : 57) has pointed out that the holotype skull is probably a female, so the females were horned and one may expect horn cores of males to be larger.

Other specimens in London are a complete left horn core BM(NH) M 14514 (Leakey 1965 : 58; pl. 71), the distal part of a horn core M 14515, a frontlet with basal halves of both horn cores M 21455, the base of a right horn core M 14520, and the base of a left horn core M 14528 which were all found in Bed I in 1931. Two incomplete horn cores, M 14540 and M 14550, came from Bed I in 1932, and the base of a right horn core M 29416 from the surface of SC II in 1935. A frontlet with horn core pedicels, M 14529 from Bed I, is also probably *P. altidens*. In Nairobi a horn core F.953 and the base of a left horn core F.1011 were Bed I surface finds in 1941. The horn core FLKN I 637, referred to as an adult giraffid of the okapi type by Leakey (1965 : 35), is in fact a *P. altidens* horn core found in 1960 and has been identified as such by Dr Leakey on its accompanying card. The horn core 1960.749 P.P.R.9 from FLKNN I which was noted as probably Caprini by Leakey (1965 : 68 (b)) is more likely to be the distal half of a *P. altidens* horn core.

The species is most numerous at FLKN near the top of Bed I, but is also represented by seven horn core pieces and other remains at FLK lower in Bed I, and by a single horn core from DK near the base of Bed I. The DK horn core, 068/6696 from the right side, differs from the FLKN ones by being shorter, more backwardly curved, having slight transverse ridges on the upper anterior surface, and by the swelling at the base being smaller and more localized posteromedially (not medially) at the junction of the horn core proper and pedicel. The FLK horn cores show some advance towards those of FLKN in having their backward curvature restricted to the more distal parts of the horn core (Pl. 17). This may be an example of infraspecific evolution of horn cores in the fairly short period during which the Bed I deposits were accumulated at Olduvai. However, other explanations are possible, such as local distributional changes of contemporaneous subspecies, and in any case one would like more than the one horn core from DK.

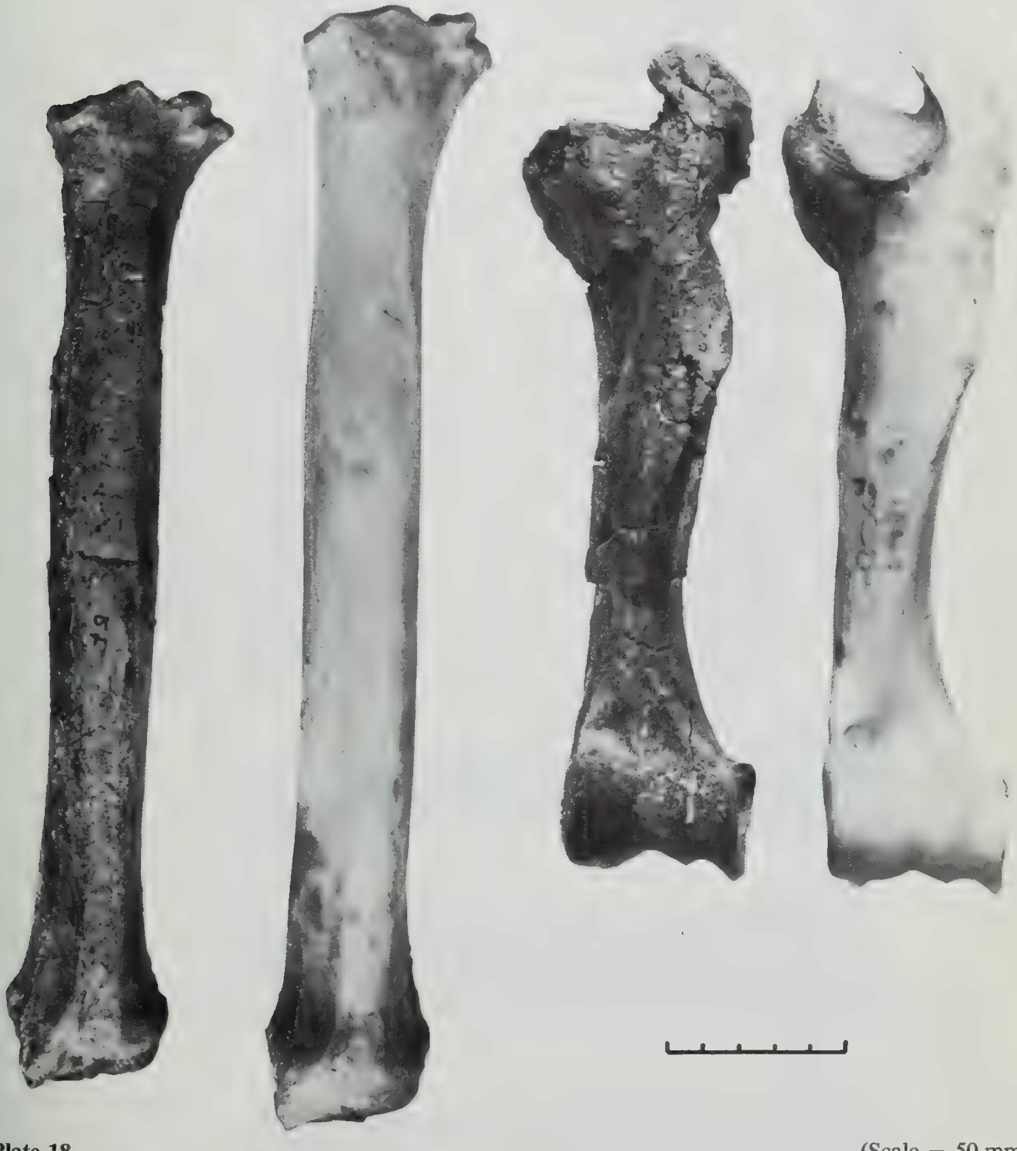


Plate 18 (Scale = 50 mm)

Anterior views of right limb bones of ***Parmularius altidens*** compared with Recent hartebeest. From the left: ***Alcelaphus buselaphus***, humerus; ***Parmularius altidens***, humerus, FLKN I 7070; ***Alcelaphus buselaphus***, radius; ***Parmularius altidens***, radius, FLKN I 2+57.

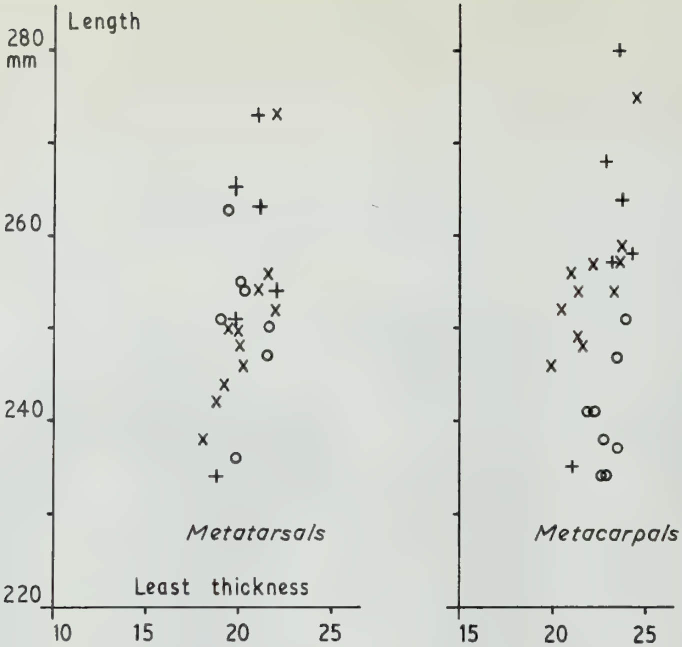


Fig. 24 Metapodial proportions in *Parmularius altidens*.
O = *P. altidens*, X = *Alcelaphus buselaphus*, + = *Damaliscus lunatus*. The metacarpals, but not metatarsals, of *P. altidens* are shorter than in the living alcelaphines.

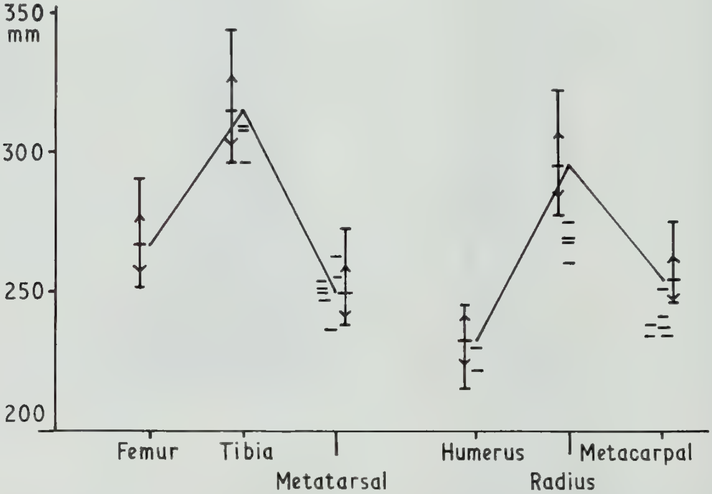


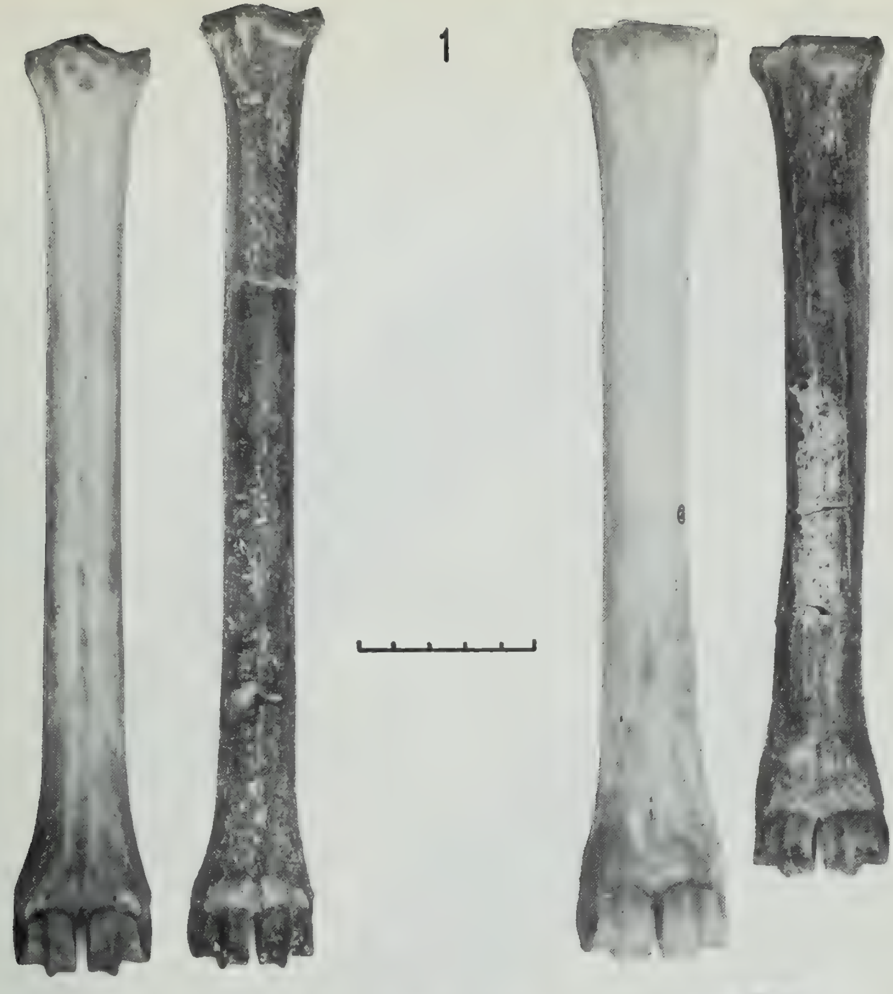
Fig. 25 Lengths of limb bones in *Parmularius altidens* and living *Alcelaphus buselpahus*. Horizontal dashes show individual readings of the right side for *P. altidens*. Means, ranges and standard deviations are shown for 11 *A. buselaphus*, and the means have been joined up. *Damaliscus lunatus*, not shown here, has proportions very like *A. buselaphus*.

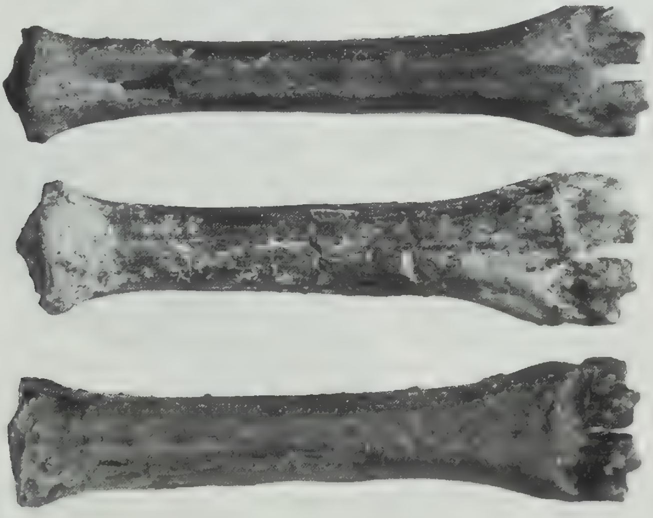
Plate 19 (Scale = 50 mm)

Fig. 1 Limb bones of ***Parmularius altidens*** compared with those of Recent hartebeest in anterior view. From the left: ***Alcelaphus buselaphus***, right metatarsal; ***Parmularius altidens***, right metatarsal, FLKN I 88; ***Alcelaphus buselaphus***, right metacarpal; ***Parmularius altidens***, right metacarpal, FLKN I 8836.

Fig. 2 Short metapodials of ? **Caprinae** sp. from FLKN I. From bottom upwards: left metacarpal, 9394; left metatarsal, 068/6665; right metatarsal, 067/1009.

1





2

The dentitions of *P. altidens* (Pl. 30, fig. 2; Pl. 37, fig. 5) are slightly smaller than in the living hartebeest. The teeth are like those of living *Alcelaphus* and *Damaliscus* in the rounded medial lobes of the uppers and lateral lobes of the lowers, and in the prominence of the ribs on the lateral walls of the uppers. On the whole, however, the central cavities of the upper molars are not quite so recurved laterally as in living *Alcelaphus* and *Damaliscus*, and the outline of the central cavities of the upper and lower molars is less complicated, though individual teeth cannot always be distinguished from *Alcelaphus* or *Damaliscus*. *P. altidens* in Bed I already has a shorter premolar row than in the Beds III–IV herd of *Damaliscus agelaius* (Fig. 22); often the molar row of *D. agelaius* is absolutely shorter, as well as relatively, than in *P. altidens*. The short premolar rows of *P. altidens* were noted by Pilgrim (1939 : 70). On *P. altidens* mandibles FLK I D.42, FLK I E.129 and FLKN I 1109 there is no alveolus in the jaw for a P_2 so that P_2 was missing in life, but on FLK I G.361, FLKN I 38, FLKN I 208, FLKN I 1198 (right) and probably FLKN I 1728 P_2 or its alveolus is still present.

The many limb bones of *P. altidens* at FLKN I show some differences from those of living *Alcelaphus buselaphus* and *Damaliscus lunatus*. The tibiae have a shorter medial malleolus at the distal end than in most individuals of the living species, and on the metacarpals there is less of an anteromedial sharply angled corner on the magnum–trapezoid facet proximally (Fig. 23). The tibiae and humeri may be shorter than in *A. buselaphus* or *D. lunatus*, the radii and metacarpals are definitely shorter and more robust, but the metatarsals are as long (Figs 24, 25; Pls 18; 19 fig. 1). Thus *P. altidens* would not have been so high at the shoulders as living alcelaphines.

MEASUREMENTS. Measurements on the skull BM(NH) M 14689 of *P. altidens* are:

Skull length from front of the premaxillae to back of the occipital condyles	*c.* 337
Anteroposterior diameter of horn core at its base	30·9
Mediolateral diameter of horn core at its base	27·4
Minimum width across lateral surfaces of horn core pedicels	72·2
Width across lateral edges of supraorbital pits	*c.* 55·6
Height from the maxilla edge between P^4 and M^1 to the maxilla–nasal boundary immediately above at 90° to the tooth row	61·3
Maximum braincase width	83·5
Skull width across mastoids immediately behind external auditory meati	108·7
Distance from rearmost point of occlusal surface of M^3 to back of occipital condyles	139·3
Occlusal length M^1–M^3	64·8
Occlusal length M^2	*c.* 23·2
Occlusal length P^2–P^4	28·3
Occlusal length M_1–M_3	69·1
Occlusal length P_2–P_4	27·7

Measurements on frontlet FLK I Balk 126 + 199 of *P. altidens* are:

Length of horn core along its front edge	330·0
Anteroposterior diameter of horn core at its base	48·8
Mediolateral diameter of horn core at its base	40·6
Minimum width across lateral surfaces of horn core pedicels	95·0

Measurements on seven frontlets and seven horn cores of *P. altidens* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length of horn core along its front edge	5	263·6	247·0–292·0	–	–
Anteroposterior diameter of horn core at its base	14 (left + right)	42·3	33·3– 50·3	4·3	1·14
	10 (left only)	42·3	33·3– 49·4	4·5	1·44
Mediolateral diameter of horn core at its base	14 (left + right)	36·7	30·8– 44·5	3·8	1·01
	10 (left only)	37·6	30·8– 41·6	4·1	1·29
Minimum width across lateral surfaces of horn core pedicels	4	88·6	79·4– 96·7	–	–

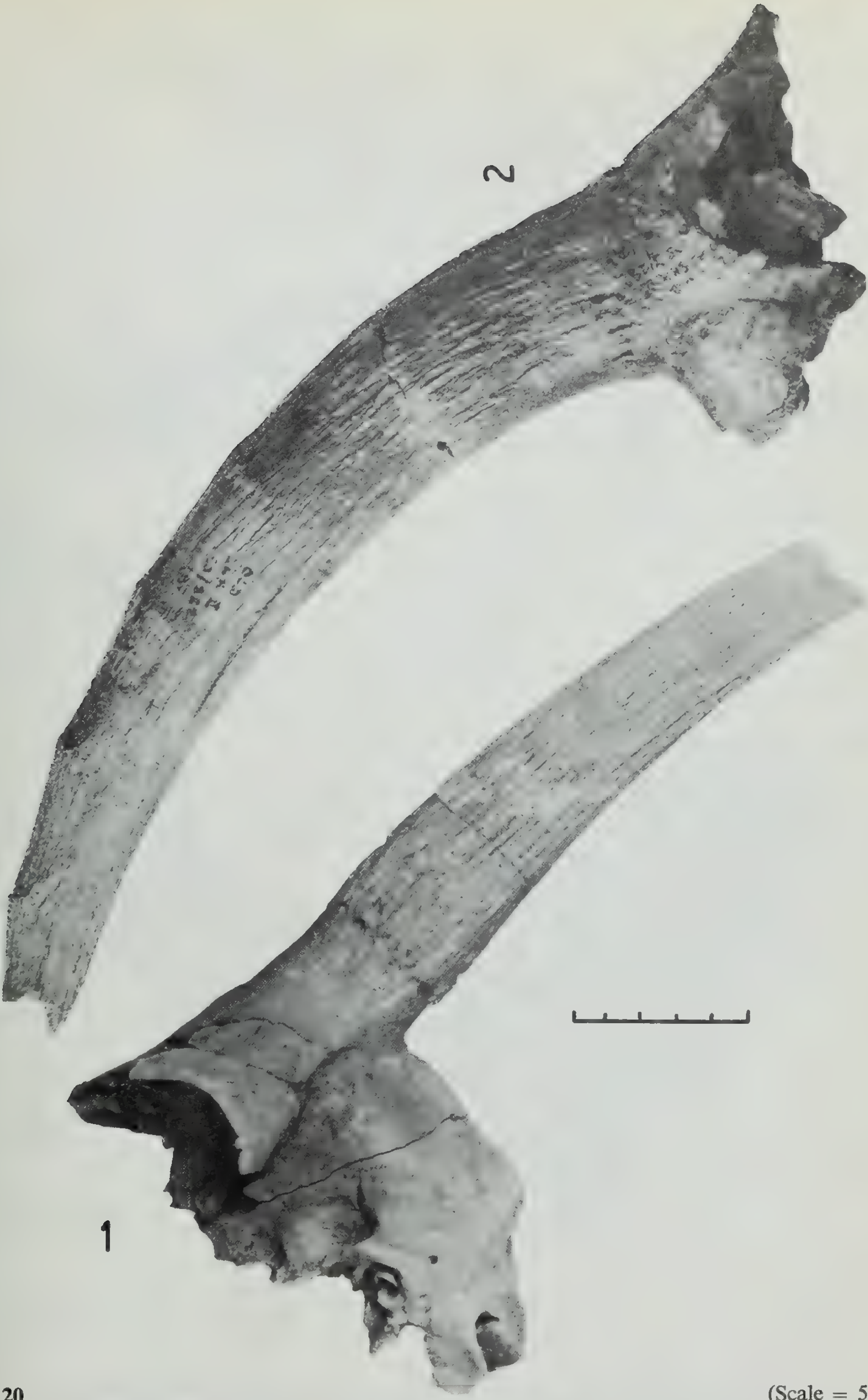


Plate 20 (Scale = 50 mm)

Fig. 1 ***Parmularius altidens.*** Lateral view of partial cranium with horn cores, HWK I 1962.068/6650.

Fig. 2 ***Damaliscus niro.*** Lateral view of right horn core, SHK II 1953.282.

Anteroposterior and mediolateral diameters at the base of other horn cores of *P. altidens* are:

DK I 068/6696	46·7 × 39·8	HWK I 1962.068/6650	46·6 × 40·0
FLKNN I surface 067/1173	37·5 × 32·3	Bed I BM(NH) M 14514	41·4 × 36·7
FLK I F.206 P.P.F.7	44·2 × 37·9	Bed I BM(NH) M 14520	45·9 × 39·2
FLK I G.232	40·4 × 34·1	Bed I BM(NH) M 14528	39·6 × 41·3
FLK I G.233 + 235 P.P.R.3	42·7 × 39·8	Bed I BM(NH) M 14540	42·4 × 38·0
FLK I C.067/1078	40·2 × 34·3	Bed I BM(NH) M 14550	42·4 × 38·3
FLK I G.067/1080	41·8 × 36·7	Bed II surface BM(NH) M 29416	47·1 × 44·1

The lengths of DK I 068/6696, FLKNN I surface 067/1173 and FLK I G.233 + 235 are 260·0, 235·0 and 305·0 mm.

Measurements on maxillae assigned to *P. altidens* are:

	FLKN I 1136	FLKN I 1604	FLKN I 10209
Occlusal length M^1–M^3	60·5	63·5	59·7
Occlusal length M^2	22·6	22·1	21·9

An immature maxilla FLKN I 430 has deciduous P^2–P^4 measuring 40·8 mm.

Measurements on 10 mandibles assigned to *P. altidens* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_1–M_3	10 (left + right)	64·6	59·4–76·1	5·2	1·65
	6 (left only)	65·2	61·5–76·1	5·6	2·27
Occlusal length M_2	10 (left + right)	20·6	18·7–23·6	1·5	0·48
	6 (left only)	20·7	19·7–23·6	1·5	0·60
Occlusal length P_3–P_4	1	18·4	–	–	–

Measurements on other mandibles assigned to *P. altidens* are:

	FLK I D.42	FLK I G.361	FLK I D.067/1094	FLK I G.067/1098
Occlusal length M_1–M_3	66·0	65·5	60·7	65·6
Occlusal length M_2	20·6	21·1	19·1	20·8
Occlusal length P_3–P_4	21·5	–	–	–

The M_2 on mandible FLKNN I 733 measures 23·0. Immature mandible FLKN I 10212 has deciduous P_4 measuring 23·4 mm.

Measurements on 14 metatarsals assigned to *P. altidens* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length	14 (left + right)	253	236–270	8·6	2·31
	7 (left only)	255	245–270	9·1	3·43
Least thickness	14 (left + right)	19·5	17·0–21·5	1·3	0·34
	7 (left only)	18·9	17·0–20·9	1·3	0·50

Measurements on 15 metacarpals assigned to *P. altidens* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length	15 (left + right)	241	234–251	5·6	1·46
	8 (left only)	242	234–249	5·0	1·76
Least thickness	15 (left + right)	22·4	20·4–24·0	1·1	0·28
	8 (left only)	21·8	20·4–23·2	1·1	0·33

Measurements of length and least thickness on other limb bones assigned to *P. altidens* are:

Tibiae	FLK I F.138 + 141	309 × 26·7	FLKN I 7074	308 × 26·8	FLKN I 7084	296 × 24·2
Humeri	FLKN I 7070	230 × 27·7	FKLN I 067/515	210 × 26·3		

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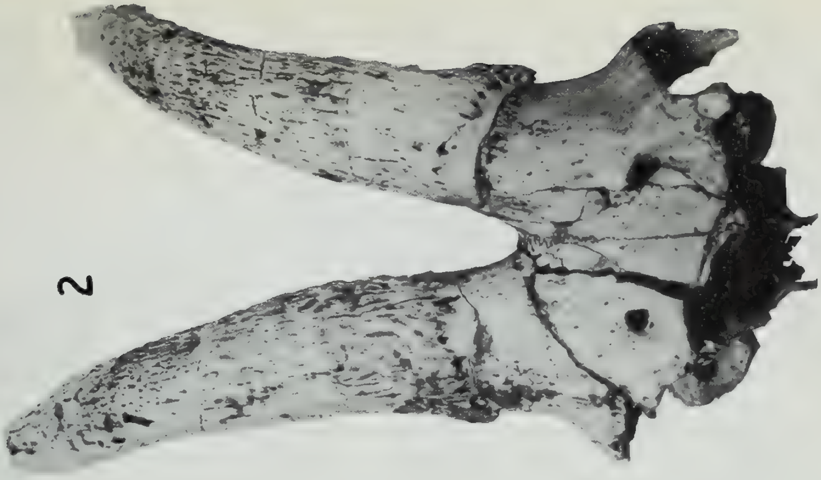

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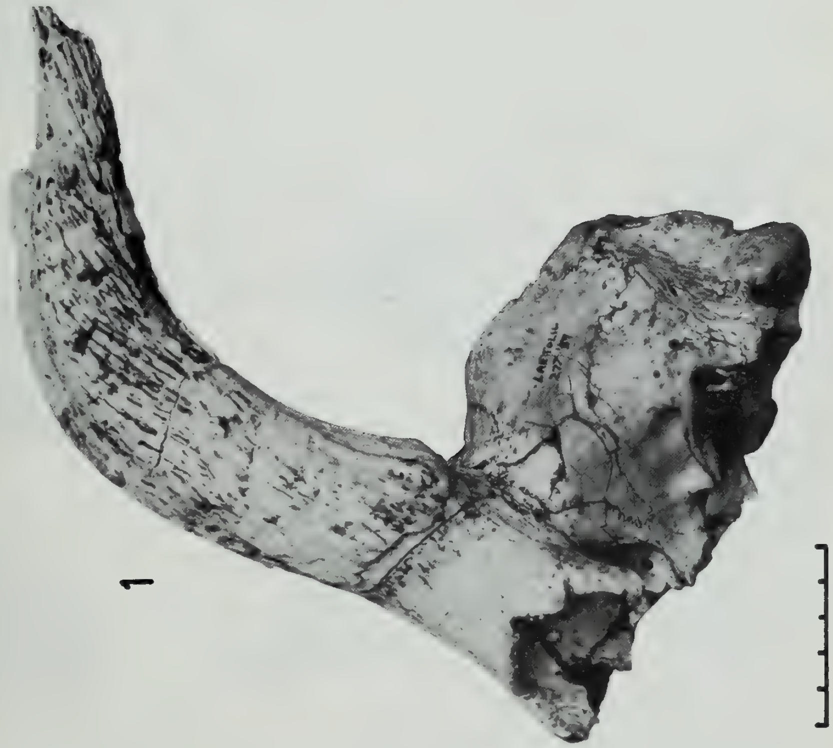


Plate 21 (Scale = 50 mm)

Fig. 1 ? ***Parmularius*** sp. Lateral view of cranium from Laetolil, 1959.277.

Fig. 2 Anterior view of same.

Radii	FLKN I 2+57	269 × 27·1	FLKN I 688	260 × 26·7	FLKN I 1046	266 × 28·4
	FLKN I 7779+7780	266 × 27·7	FLKN I 8247	283 × –	FLKN I 067/4741	268 × 28·3
Metacarpal	DK I 76	236 × 24·7				

An associated set of limb bones from DK I, humerus 141 222 × 26·2, radius 58 275 × 26·2 and metacarpal 143 241 × 22·0 mm.

Comparisons. The lower half of a left horn core F.161-37 found in 1972 represents *P. altidens* in member H of the Shungura Formation at Omo.

A well-preserved cranium 1959.277 with most features intact, but damage like that caused by *Ceratophaga vastella* on the front of its horn cores from Laetolil (Pls 21; 22, fig. 2), may be ancestral to *Parmularius altidens*. That it is an alcelaphine is shown by the small supraorbital pits, a low parietal boss, high level of frontals between the horn core bases and a central longitudinal groove on the basioccipital. It could well be primitive in the rather long and little-angled braincase, the close supraorbital pits with a concave surface of the frontals in between them instead of a convex one, and the straight parietofrontals suture behind the horn core bases.

All the characters so far mentioned could be expected in an ancestor of *P. altidens*, although the low parietal boss and the primitive characters bar it from admission to that species. It is additionally different from *P. altidens* in having more uprightly inserted horn cores and localized posterolateral swellings at the base of the horn cores. It does have an occipital surface with strong laterally-facing components which is like *P. altidens*, and might also be primitive. The horn cores curve back fairly abruptly just over half way from base to tip, and there is some similarity between them and the *P. altidens* horn core 068/6696 from DK I.

Measurements on this Laetolil cranium are:

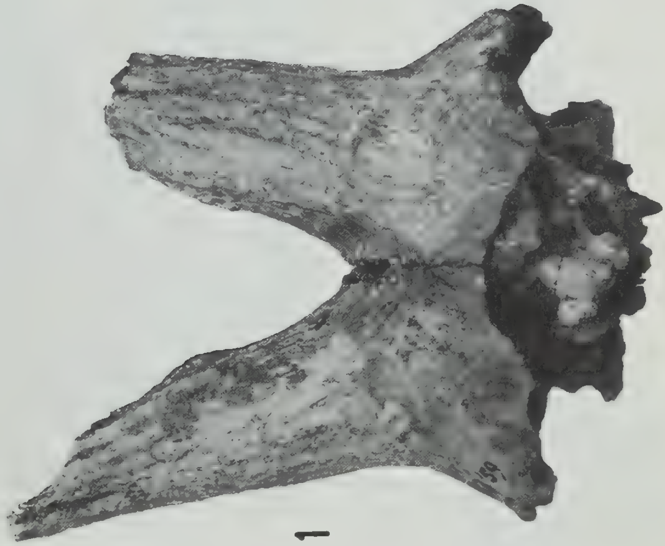
Length of horn core along its front edge	208·0
Anteroposterior diameter of horn core at its base	43·8
Mediolateral diameter of horn core at its base	38·2
Minimum width across lateral surfaces of horn core pedicels	92·8
Width across lateral edges of supraorbital pits	45·7
Length from back of frontals to top of occiput	62·3
Maximum braincase width	73·8
Skull width across mastoids immediately behind external auditory meati	94·3
Occipital height from top of foramen magnum to top of occipital crest	38·0
Width of anterior tuberosities of basioccipital	21·0
Width of posterior tuberosities of basioccipital	28·1

The right horn core from Laetolil which Dietrich (1950 : 36; pl. 2, fig. 21) called 'Reduncini gen. et sp. indet.' could be conspecific with the cranium 1959.277. Its basal diameters are 38·8 × *c.* 30·3 mm.

Parmularius angusticornis (Schwarz 1937)

1937 *Damaliscus angusticornis* Schwarz : 55, no figure.
1965 *Damaliscus angusticornis* Leakey : 51; pls 63–66.
1965 *Damaliscus antiquus* Leakey : 55; pls 67–69.
1965 *Parmularius* sp. indet. Leakey : 60; pl. 77.
1965 cf. Alcelaphini Leakey : 66(b); pl. 91.

Diagnosis. A species of *Parmularius* about the size of *Alcelaphus buselaphus* or slightly larger; horn cores more massive, with thicker bases and often more divergent in their distal parts than in *P. altidens*; most horn cores almost without backward curvature. Braincase more extremely shortened and more strongly angled on the facial axis than in *P. altidens*; parietal boss less marked than in *P. altidens*; suture of parietofrontals without a central indentation; large occipital surface retaining its median vertical ridge but facing backwards more clearly than in *P. altidens* or *rugosus*; auditory bullae small and little inflated; basisphenoid strongly bent upwards on plane of basioccipital.



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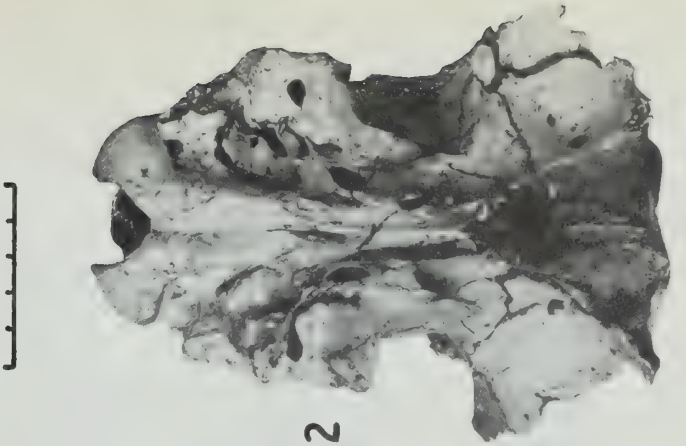

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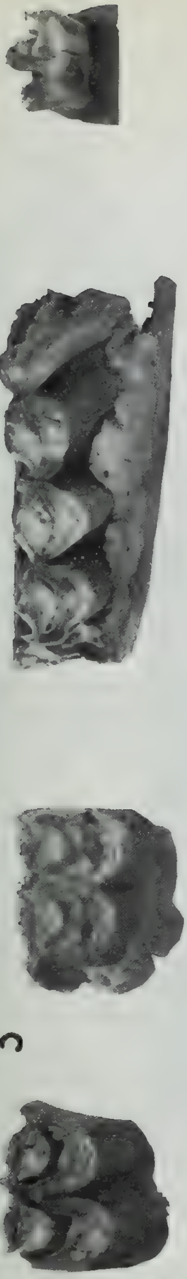

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Plate 22 (Scale = 50 mm for cranial pieces and 25 mm for teeth)

Laetolil fossils

Fig. 1 **Alcelaphini** sp. indet. Anterior view of frontlet, 1959.233.

Fig. 2 ? ***Parmularius*** sp. Ventral view of cranium, 1959.277.

Fig. 3 ? **Hippotragini.** Occlusal view of teeth. From the left: left upper molar 1959.454, right upper molar 1959.453, part of left mandible 1959.56, right P_4 1959.456.

PARATYPE. The holotype was a crushed cranium formerly in Munich but unfortunately destroyed during the Second World War. However, Schwarz had nominated as paratype a partial frontlet with incomplete right horn core in London, BM(NH) M 14553, and this still exists. It was figured by Leakey (1965 : pl. 63).

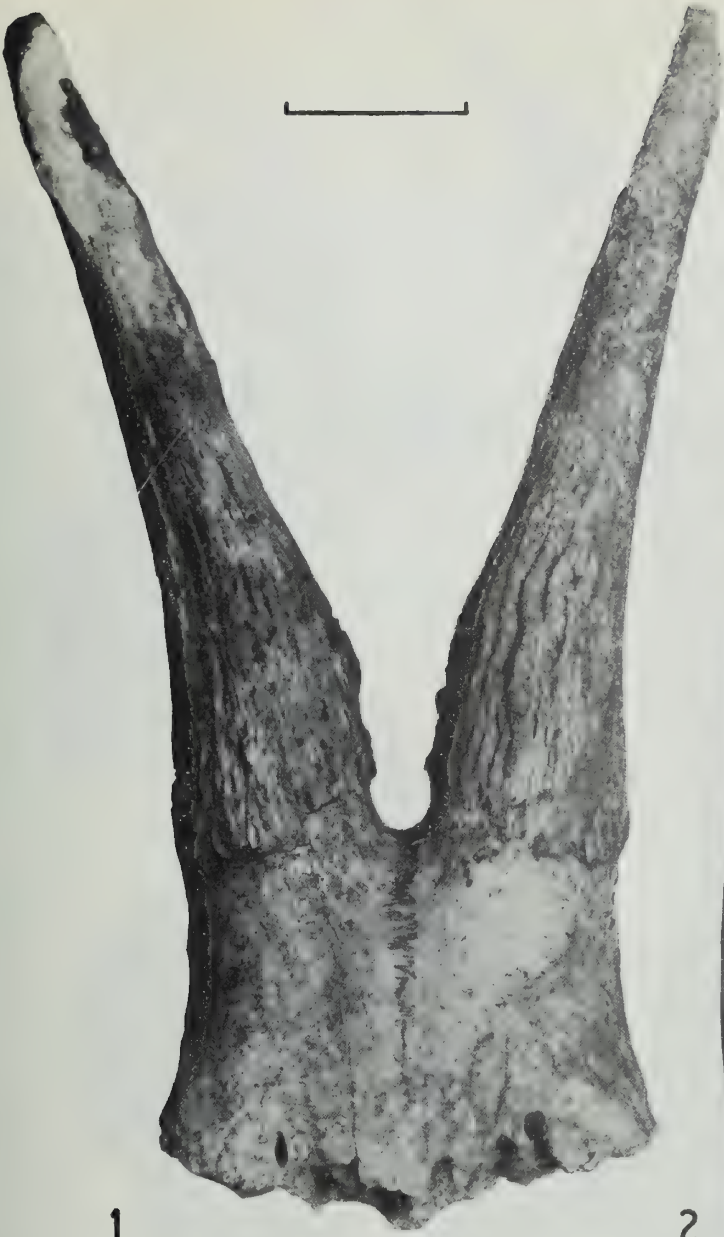
HORIZON. The paratype is from the surface of Bed II, Olduvai. Other specimens are frequent in middle and upper Bed II. The species is also known from Peninj, Isimila and Kanjera.

REMARKS. This is the largest and morphologically the most advanced species of its genus. It is known only by horn cores and crania. Leakey (1965 : 51) drew attention to the deficiencies of Schwarz's original definition, revised it and figured the paratype. He also described and figured other conspecific specimens: a cranium M 21425 (pls 64–65) found in 1935 *in situ* at SHK II, a frontlet M 21422 (pl. 66) from the surface at VEM in 1935 and a frontlet M 21423 from the surface of SHK II in 1935.

Leakey (1965 : 55) also founded an allied species which he called *Damaliscus antiquus*. The holotype cranium (numbered and catalogued P.P.T.1, not P.P.T.3 as given by Leakey 1965 : 55, pl. 67) was excavated from BK II in 1955, but the paratype cranium BM(NH) M 21428 was found being eroded out at VEK in 1935 and taken to be of Bed I age. However, 'VEK II' is written on the back of the left horn core, while the inscription 'VEK I' on the side of the braincase seems to have been added more recently, perhaps at the time of registration. It is this record which was thought to establish the species as older than *angusticornis*, so that *antiquus* was a fitting trivial name. Three further specimens in Nairobi were a left horn core from SHK II *in situ* 1957.1284, and the base of a left horn core F.963 P.P.R.4 and the basal half of a right horn core with mid-frontal suture and orbital rim F.948, both found on the surface in 1941. *D. antiquus* was said to differ from *D. angusticornis* in the horn cores being inclined slightly backward from the forehead, curving slightly outwards and backwards and then forwards, not tapering so rapidly, without such an abrupt change in cross-section, and sometimes having traces of cross ribbing. The alcelaphine groove (postcornual fossa) of *antiquus* appeared shallower and less well-defined, but with a sharp anterior edge, and the flat-topped protuberance in the centre of the parietals was stronger. The skulls appeared generally larger and more rugose.

The curving of the horn cores slightly outwards and backwards and then forwards is well shown on the paratype of *D. antiquus* (Leakey 1965 : pls 68, 69) but not on the holotype (pl. 67), and this condition is also approached by the *angusticornis* paratype (pl. 63). The larger size and greater rugosity is less true of the *antiquus* paratype than of the holotype. It is also apparent that the assignment of some horn cores excavated from BK II since 1960 is a matter of difficulty; they are without rapid tapering above the base, just as in *antiquus*, but are straight as in *angusticornis*, and while two of them (1963.2499 and 1963.067/1650) have cross ribbing, the other two (1963.3178 and BK II East 1961.068/6660) have not. Other Olduvai pieces are also difficult to place. A damaged frontlet 1962.068/6648 from Long K East, middle Bed II, agrees with *angusticornis* in the abrupt and sudden tapering of its horn cores shortly above the base, but with *antiquus* in their slight inclination backwards and in having a flat-topped parietal protuberance. A cranium BM(NH) M 21429 found at VEK ? II in 1932 (Leakey 1965 : 66(b); pl. 91) resembles *antiquus* in the absence of a marked basal swelling, but the horn cores are straighter than *antiquus* is said to have. A left horn core 1960.068/6126 from the surface of HWK II is larger than the *antiquus* holotype but agrees with *angusticornis* in its pronounced basal swelling, although the postcornual groove is shallow.

It seems then that the two species cannot be distinguished on the wider range of specimens now available, and the prior name is *angusticornis*. We place this single species in *Parmularius* instead of *Damaliscus* because of the thickened bases of its horn cores, the lack of a markedly wide separation of the supraorbital pits, its parietal boss and the very short and strongly inclined cranial roof. All the Olduvai specimens of known horizon are from middle and upper Bed II with the doubtful exception of M 21428. Two crania in Nairobi from unknown horizons are the surface finds F.3015 and 068/5854. Bed II surface finds in 1941 are the left horn core bases F.973, F.3005 and 068/5927, right horn core bases F.948, F.975, F.3005 and 068/5926, and a frontlet with the basal halves of both horn cores F.989. A possible juvenile specimen is represented by a left horn



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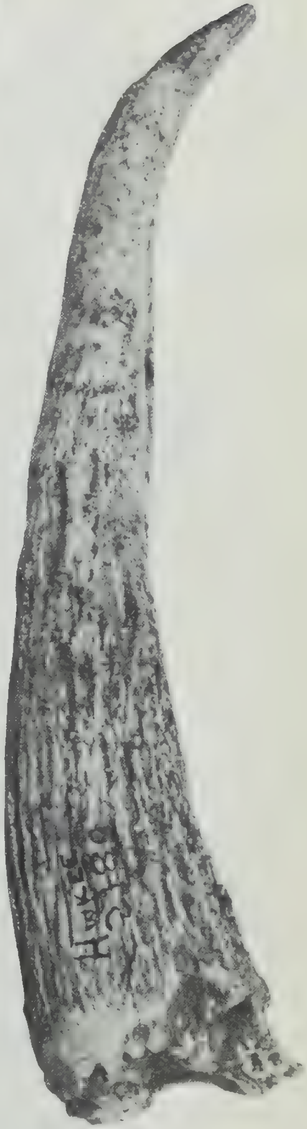

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Plate 23 (Scale = 50 mm)

Parmularius angusticornis

Fig. 1 Anterior view of frontlet, HWK EE II 1972.172.

Fig. 2 Medial view of right horn core, HWK EE II 1972.2180.

core F.3003 found on the surface in 1941. We were unable to find the cranium with horn cores from BK II East mentioned by Leakey (1965 : 55) in either Nairobi or Dar es Salaam. We have seen three fine pieces found in 1972 at HWK EE in middle Bed II. 172 and 635 are frontlets with complete horn cores, and 2180 is a complete right horn core (Pl. 23). The horn cores are almost straight in side view but with a very slight forward curvature in their distal half and a tiny backward bend at their tip.

Four interesting specimens from BK II are a partial frontlet with complete right horn core 1963.2499 (Pl. 25, fig. 3), a frontlet with nearly complete horn cores 1963.3178 (Pl. 24), a left horn core 1963.067/1650 and a complete right horn core BK II East 1961.068/6660. The first three are very long and not large in relation to the underlying skull parts. The basal thickening is not pronounced and is no more developed than in *P. altidens*, although here the thickening is of

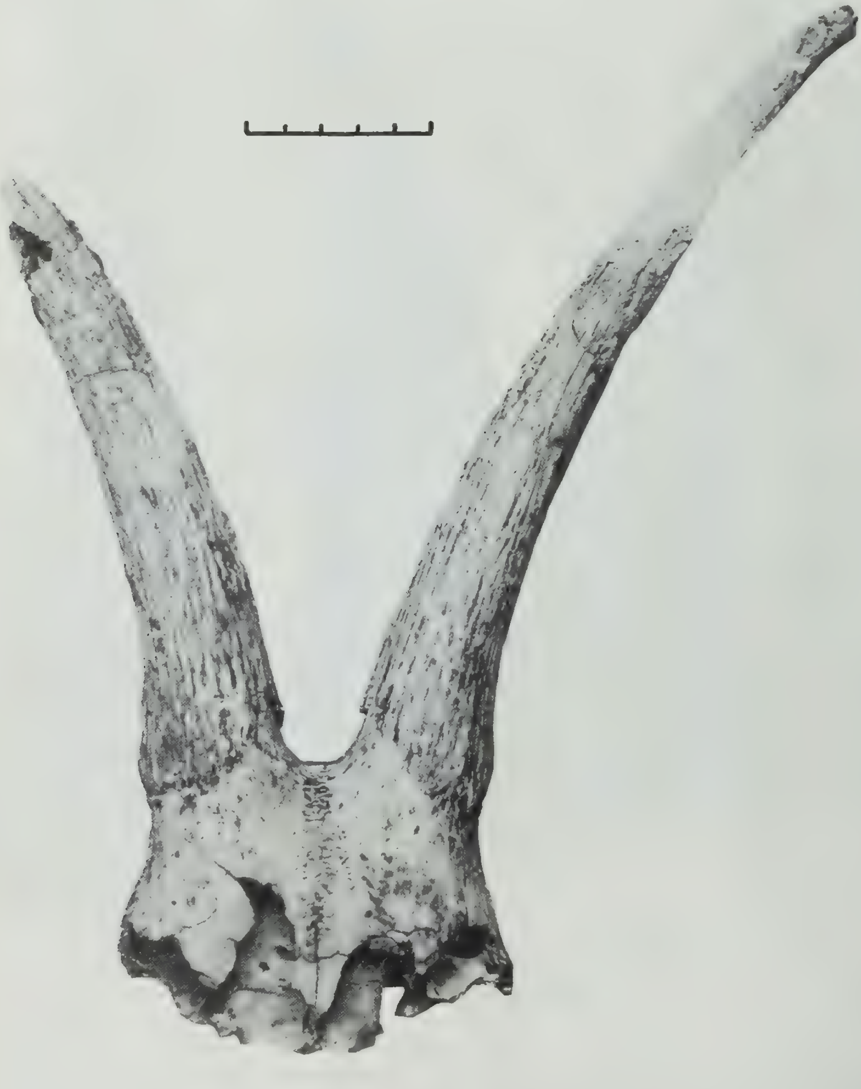
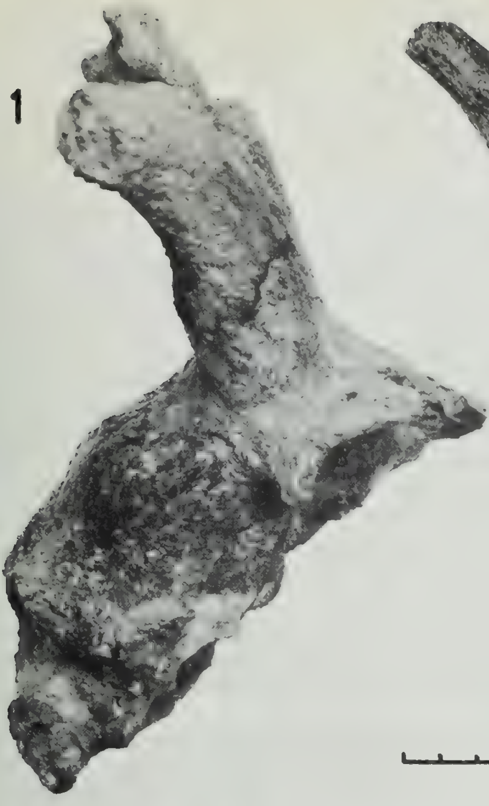
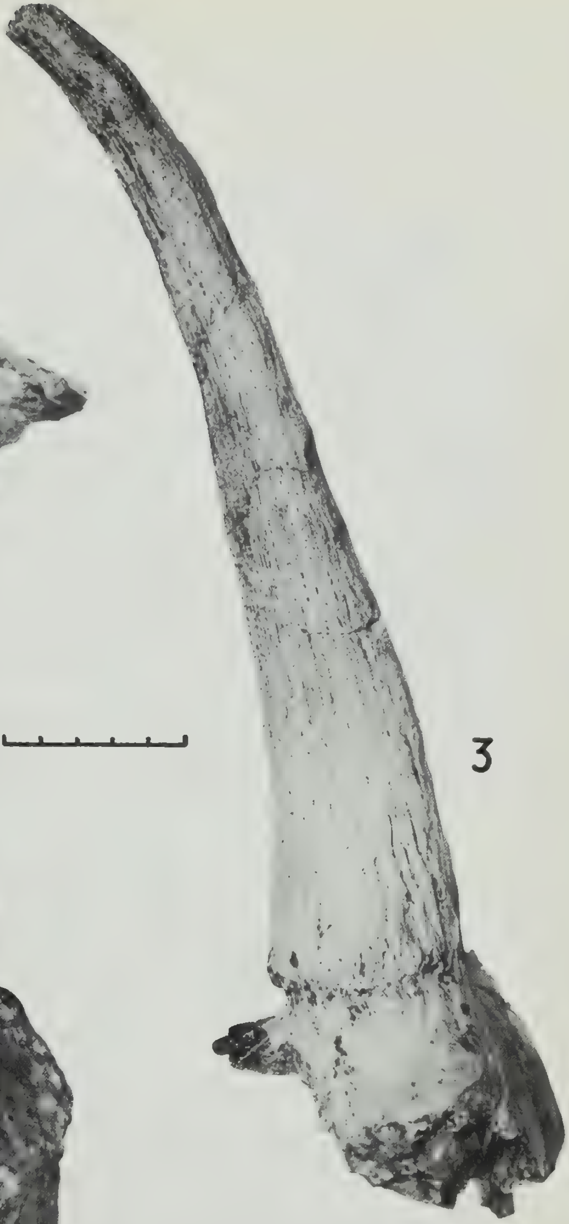


Plate 24 (Scale = 50 mm)

Parmularius angusticornis. Anterior view of frontlet, BK II 1963.3178.





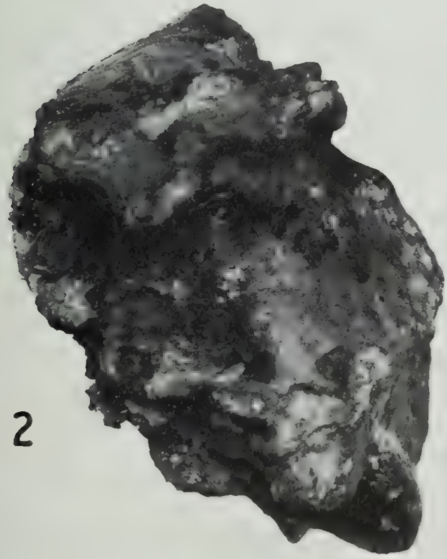


Plate 25 (Scale = 50 mm)

Fig. 1 ***Damaliscus agelaius.*** Lateral view of cranium S.38 from Bed II.

Fig. 2 ***Parmularius altidens/angusticornis.*** Lateral view of cranium, FLKN II 1960.067/4951.

Fig. 3 ***Parmularius angusticornis.*** Lateral view of right horn core, BK II 1963.2499.

the whole horn core base rather than on the medial side, and the outer surface is more flattened just above the base. In side view the back of the horn core bases project rather markedly beyond the pedicels, again unlike *P. altidens*. There are pronounced transverse ridges in two of them, as already mentioned. Both 1963.2499 and 1963.3178 show increasing divergence towards the tips like SHK II 1957.1284, and the tip of 1963.2499 has an abrupt backward and outward twist. The fourth horn core, 068/6660, is very similar but somewhat shorter. Probably all these horn cores are of females.

Further specimens in London are the right horn core bases M 14547 from Bed II in 1931 and M 14525 said to have come from Bed I in 1931, the distal part of a horn core M 14552 from the surface of Bed II in 1931, a right horn core base with part of the frontal M 21424 from the surface of SHK II in 1935, the basal part of a left horn core M 21426 from the surface of DC II in 1935, most of a left horn core M 21427 found in 1935, a right horn core base M 29416 from the surface of SC II in 1935 and a number of unregistered horn cores which were surface finds in 1935 (two left horn cores from SC II, a left base from DC II, a left horn core and part of a right from BK II, a left horn core from MRC II and an incomplete right horn core from GHTK II). The small basal diameters of M 29416 give it an appearance like *P. altidens*. Two other London horn cores can be tentatively identified as *Parmularius* sp.; these are a horn core tip M 14523 from Bed I in 1931 and the base of a right horn core M 14538 from Bed I (according to its label and the register) or Bed II (written on horn core) in 1932.

A left horn core F.3001 P.P.F.5 in Nairobi, marked 'Bed II *in situ*' and recorded as *Parmularius* sp. indet. by Leakey (1965 : 60; pl. 77), can perhaps be regarded as a male *P. angusticornis*. It has little basal swelling and is larger and less transversely compressed than BK II specimens, with slightly more curvature, but has the same amount of divergence. The orbital rim is preserved, the parietal is very short and there is a small parietal boss. The specimen is clearly not hippotragine by the angle of the braincase on the frontal, too little transverse compression and the outward divergence of the horn core.

We believe that *Parmularius angusticornis* could be the direct congeneric descendant of *Parmularius altidens*. It differs from *P. altidens* in having larger and straighter horn cores and a more extremely shortened braincase (Fig. 26), the latter brought about either by posterior movement

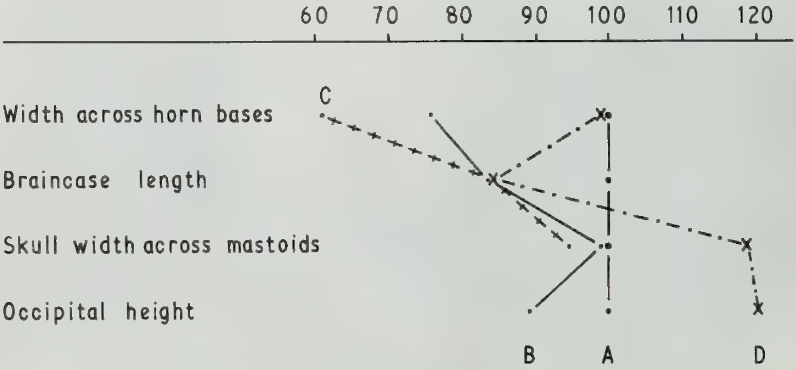


Fig. 26 Percentage diagram of skull measurements in some alcelaphines.

A = standard line at 100% for mean of 12 east African *Damaliscus lunatus*,
B = mean of 14 east African *Alcelaphus buselaphus cokei*,
C = *Parmularius altidens* holotype,
D = mean of 6 *P. angusticornis*: BK II 1955.P.P.T.1, 068/5854, F.3015, BM(NH) M 21428, M 21425, and Isimila cranium.

Braincase length is measured from the back of the frontals to the occipital top. *A. b. cokei* has closer horn core insertions, a shorter braincase and a lower occipital than *D. lunatus*. *P. altidens* has very close horn core insertions (connected with the small size of its horn cores) and a short braincase. *P. angusticornis* has a short braincase and a large occipital surface.

of the horn core insertions or by reorientation of the brain cavity internally. A possible intermediate stage is given by a cranium 1960.067/4951, with pieces of its horn cores 1960.067/4949, 067/4946 and 067/4948, from FLKN II 10 ft (3·05 m) above the base of Bed II (Pl. 25, fig. 2). It has the braincase top less shortened and less angled on the facial axis than in the SHK II and BK II *P. angusticornis*.

Leakey (1965 : 51), following Schwarz, placed *P. angusticornis* in *Damaliscus* but wrote 'there is no evidence to suggest that it is in any way ancestral to the living members of the genus. It has some characters that are nearer to *Alcelaphus* than to *Damaliscus*.' It is apparent that *Parmularius angusticornis* resembles *Alcelaphus* more than *Damaliscus* in the angle of nearly 90° between the planes of the frontals and the top of the braincase, the top of the braincase being set so steeply, and the extreme posterior position of the orbits; all these characters are linked with one another. Other resemblances to *Alcelaphus* are the horn core insertions being in the same plane as the face in side view, and the long distance of the horn core bases above the orbital rims. (In *A. buselaphus* the last character arises from the union of the horn core pedicels.) *Parmularius altidens* shows some of these resemblances: the obliquely inserted horn cores, long pedicels, horn cores parallel at least at their bases, and the characters connected with braincase shortening although at a less advanced stage. However, *Parmularius* is very unlikely to be ancestral to *Alcelaphus* because of its small preorbital fossae and extremely short premolar rows, and because of the existence of an alternative ancestor, *Rabaticeras* (p. 410), for *Alcelaphus*.

MEASUREMENTS. Measurements on the crania of *P. angusticornis* are:

	VEK II	SHK II	BK II	
	M.21428	M.21425	1955 P.P.T.1	F.3015
Anteroposterior diameter of horn core at its base	62·0	61·4	58·1	–
Mediolateral diameter of horn core at its base	54·3	50·9	53·0	–
Minimum width across lateral surfaces of horn core pedicels	115·5	116·7	116·1	–
Width across lateral edges of supraorbital pits	64·6	–	66·6	–
Length from back of frontals to top of occiput	53·2	–	48·7	–
Maximum braincase width	100·5	–	103·0	101·0
Skull width at mastoids immediately behind external auditory meati	144·0	–	–	137·0
Occipital height from top of foramen magnum to top of occipital crest	–	59·6	58·4	60·9
Width of anterior tuberosities of basioccipital	29·1	–	–	32·9
Width of posterior tuberosities of basioccipital	46·9	–	–	40·7

Measurements on the two most complete frontlets of *P. angusticornis* are:

	HWK EE II	HWK EE II
	172	635
Horn core length	280·0	305·0
Anteroposterior diameter at horn core base	68·2	66·1
Mediolateral diameter at horn core base	60·0	58·7
Minimum width across lateral surfaces of horn core pedicels	123·4	119·0
Width across lateral edges of supraorbital pits	73·4	–

Measurements on other frontlets of *P. angusticornis* are:

	VEK II	LONG K E II	SHK II	BK II	
	M.21422	068/6648	M.21423	1963.3178	068/5854
Anteroposterior diameter at horn core base	61·8	69·3	54·5	46·8	54·0
Mediolateral diameter at horn core base	55·1	57·4	43·8	38·4	45·6
Minimum width across lateral surfaces of horn core pedicels	127·4	126·4	113·6	90·5	116·1

Anteroposterior and mediolateral diameters at the base of other horn cores and one measurement of length on a horn core of *P. angusticornis* are:

HWK EE II 2180	63·0 × 59·1, length 340·0	BK II 1963.067/1650	45·2 × 40·8
SHK II 1952.598	52·7 × 41·5	BK East II 1961.068/6660	46·0 × 40·8
SHK II 1957.945	57·6 × 48·7	Bed II F.3001 P.P.F.5	57·0 × 52·1
SHK II 1957.1284	62·6 × 52·7	Bed II surface BM(NH) M 14553	58·0 × 49·5
BK II 1963.2499	57·4 × 44·9	BM(NH) M 21427	65·0 × 54·1
BK II 1963.2813	45·0 × 39·7		

COMPARISONS. *Parmularius angusticornis* is represented at Peninj by the basal parts of left horn cores A67.254 (WN64.12.CFG III.MZ) and A67.253 (WN64.110.RDG.S), and a right horn core A67.243 (WN64.214.TMG(U)?MZ), and possibly by other pieces. The anteroposterior and mediolateral diameters at the base of A67.243 are 60·5 × 55·0 mm.

Several pieces of *P. angusticornis* are known from Kanjera. BM(NH) M 15855 is the base of a horn core identified as *Alcelaphus kattwinkeli* by Hopwood (*in* Kent 1942 : 126), and there are also the distal ends of two more horn cores M 25626 and M 25722. The latter is preserved to the tip where it shows a sharp and localized backwards and inwards bend. M 25720 is a horn core base more doubtfully of *P. angusticornis*.

P. angusticornis is known from Isimila (Coryndon *et al.* 1972), a site in southern Tanzania equated with upper Bed IV of Olduvai by its Acheulian artefacts and perhaps about a quarter of a million years old (Howell & Clark 1963 : 482 and their references; Howell *et al.* 1972). This occurrence would therefore postdate its Olduvai record. The species is represented by a well-preserved cranium with both horn cores, at present in the Nairobi collections but eventually to be housed in Dar es Salaam.

Measurements on the Isimila cranium are:

Anteroposterior diameter of horn core at its base	59·7
Mediolateral diameter of horn core at its base	53·2
Minimum width across lateral surfaces of horn core pedicels	121·7
Length from back of frontals to top of occiput	56·3
Maximum braincase width	106·0
Skull width across mastoids immediately behind external auditory meati	130·0
Occipital height from top of foramen magnum to top of occipital crest	57·0
Width across posterior tuberosities of basioccipital	40·9

Langebaanweg horn cores previously recorded as *P. angusticornis* (Gentry *in* Hendey 1970a : 116) are now known to have been incorrectly identified. Subsequent finds show that not all horn cores have such clear basal swellings. Other characters are also unlike *P. angusticornis*: horn cores often curving more backwards, braincase roof less sharply angled, frontals lower between horn core bases and supraorbital pits closer together. In any case all the Langebaanweg alcelaphine teeth are less advanced than in Olduvai Bed II, and the fauna must be substantially earlier in age.

An incomplete cranium with both horn core bases, 1959.233 from Laetolil (Pl. 22, fig. 1) at present in Nairobi, has some resemblance to *P. angusticornis*. The horn cores arise close together beside the midfrontal suture and diverge at about 40°. The basioccipital, basisphenoid and a part of the occipital surface are present, but not the occipital condyles. It differs from *P. angusticornis* in the smaller size of its horn cores, their more upright insertions in side view, the insertions being less far above the level of the orbits or the supraorbital pits, the longer braincase roof less inclined downwards, there being no sign of a parietal boss, and in the narrower cranium. It could be related to the Langebaanweg species just mentioned, except that Laetolil alcelaphine teeth are more advanced than those at Langebaanweg. It is unlikely to be related to later *Parmularius* if the Laetolil skull 1959.277 (p. 382) is ancestral to *Parmularius*. 1959.233 differs from 1959.277 in its larger size, the slight forward bending indicated by the back of the right horn core, the absence of a parietal boss and the wider supraorbital pits.

Measurements on the Laetolil cranium 1959.233 are:

Anteroposterior diameter at base of horn core	47·6
Mediolateral diameter at base of horn core	42·7
Minimum width across lateral surfaces of horn core pedicels	110·1
Width across anterior tuberosities of basioccipital	25·2
Width across posterior tuberosities of basioccipital	33·8

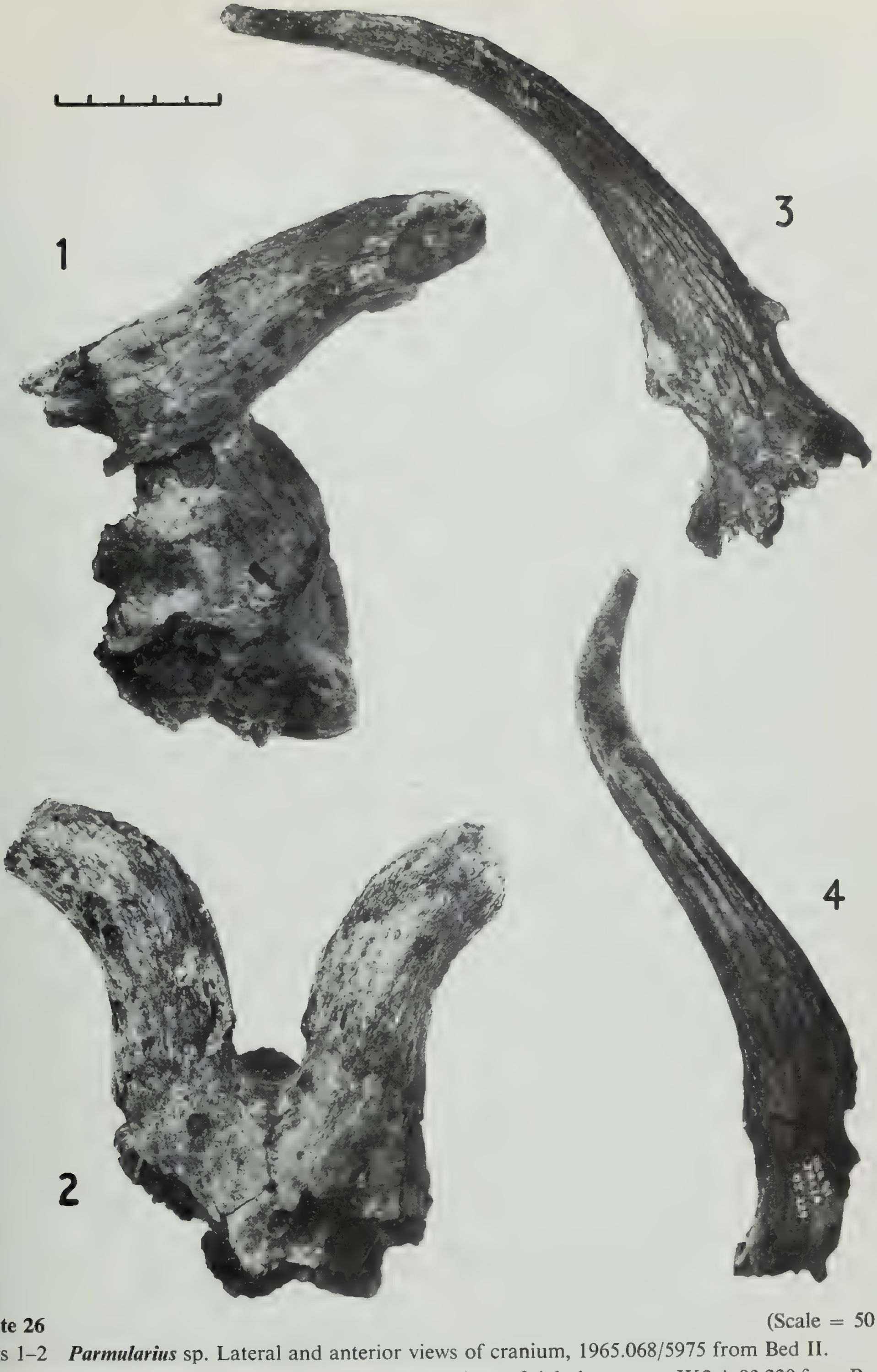


Plate 26 (Scale = 50 mm)

Figs 1–2 ***Parmularius*** sp. Lateral and anterior views of cranium, 1965.068/5975 from Bed II.

Figs 3–4 ***Parmularius rugosus.*** Lateral and anterior views of right horn core, JK2 A.03 220 from Bed III.

Parmularius rugosus L. S. B. Leakey 1965

1965 *Parmularius rugosus* Leakey : 59; pls 75–76.

DIAGNOSIS. A species of *Parmularius* about the size of *P. altidens*, but horn cores diverging a short distance above the base and having a basal posterolateral swelling. Braincase roof about as short as in *P. altidens* but with only a small parietal boss; fairly small preorbital fossae; each side of the occipital facing partly laterally; small auditory bullae; basisphenoid bent upwards less strongly than in *P. angusticornis*.

HOLOTYPE. Skull with left and right P^4–M^3, BM(NH) M 21430, found in 1932.

HORIZON. The holotype came from the base of Bed IV at HWK Castle (M. D. Leakey 1971b : 287). Other specimens are from Bed III.

REMARKS. This species is less specialized morphologically and less common as a fossil than the larger *P. angusticornis* of Bed II. Unfortunately the holotype has retained only a part of its right horn core on which the posterolateral swelling is slightly indicated. It may have lacked at least the left P^2 in life, but this is not certain. It seems to have been correctly assigned generically, as indicated by its oblique horn core insertions situated close together, the posterolateral basal swelling of the horn core, short and strongly angled braincase, small parietal boss, not very widely spaced supraorbital pits, small preorbital fossae and short premolar row.

The lack of information about horn core morphology of the holotype makes it difficult to be certain about assigning other Olduvai specimens to this species. A cranium JK2 TT1, found in 1969 in Bed III, has retained both its horn cores, and the right one is almost complete. It is best identified as *Parmularius rugosus*. The horn cores are long, not mediolaterally compressed, with no flattened lateral surface or keels, transverse ridges are present distally and a slight posterolateral basal swelling is present. They are inserted far behind the orbits, inserted obliquely in side view and close together in front view, parallel at the base then acquiring an increased divergence which diminishes at the tip, and curving backwards only distally. The braincase is very short, much bent on the face axis and with some trace of a parietal boss, the supraorbital pits not visible, and the occipital faces partly laterally as well as backwards and shows a strong, median vertical ridge with flanking hollows. The auditory bullae are inflated and of small to moderate size.

A right horn core, JK2 A.03 220 from Bed III (Pl. 26, fig. 3) may also be taken as *P. rugosus*. It is small, apparently inserted well behind the orbits, with a pronounced posterolateral swelling, diverges quite strongly and then has an inwardly recurved tip. It has no mediolateral compression. There are transverse ridges distally and a normal alcelaphine long shallow postcornual groove. Its differences from the holotype are a fairly sharp diminution in thickness above the base, and a sharp backward curvature in side view.

A larger but otherwise similar basal part of a right horn core without a number was found at SHK II in 1952. It shows the posterolateral basal swelling, backward curvature, divergence and lack of mediolateral compression, but has transverse ridges from the base upwards. Its earlier level than the last specimen must make assignment to *P. rugosus* still more tentative, particularly as another species of the same genus, *P. angusticornis*, is well known from SHK II.

A partial cranium with horn cores, 068/5975 (Pl. 26, figs 1, 2) was found in 1965 at HWK EE in black sand about 3·7 m above the Sandy Conglomerate in middle Bed II. R. L. Hay confirmed (personal communication, March 1969) that the matrix was 'pyroxene-rich volcanic sandstone with a little quartz. Some of the pyroxene is euhedral. This is very probably from Bed II above the level of the Eolian Tuff (now Lemuta) Member.' The features which suggest that this specimen is a *Parmularius* are the short braincase top strongly angled on what would have been the line of the facial axis, a small parietal boss (about as strong as in *P. angusticornis*) and the very oblique horn core insertions on long pedicels. The horn cores diverge strongly outwards a short distance above their bases, but in side view they are in the same plane throughout their preserved length, bending neither backwards nor forwards. They have no mediolateral compression. There is no sign of any basal swelling on the horn cores, but there is a hint of a posteromedial keel at the edge of the somewhat flattened posterior surface. The occipital surface has a prominent median vertical ridge, and each half of the surface has quite a strong lateral-facing component. The basioccipital is typically alcelaphine with a central longitudinal groove and anterior tuberosities less wide than the posterior ones. It differs from the 1969 JK2 III TT 1 cranium in the posteromedial keel at the base of the horn core, the abrupt bend outwards of the horn cores close to their base, the narrower basioccipital, and probably in having less upright horn core insertions. The most that can be done with this specimen is to assign it to *Parmularius* sp.

Several horn cores from lower Bed II and the lower part of middle Bed II at Olduvai belong to a small-horned alcelaphine, seemingly related to *Parmularius rugosus*. A complete left horn core 58 (Pl. 32, fig. 3), complete right horn core 067/5523 and the distal half of a right horn core 54 all came from HWK lower Bed II in 1959–60. An immature frontlet with complete right horn core and basal half of the left 068/6649 (Pl. 32, fig. 2) was found in clay above the Sandy Conglomerate (and above level 5) at HWK East II in 1962. Two frontlets with complete horn cores, 2061 and 2181, and a right horn core 954 (probably a female) were from the Sandy Conglomerate at HWK EE II in 1972. In addition we have seen a cast, kindly supplied by Mrs Mary Leakey, of a complete right horn core with a small part of the cranial roof, HWK EE II 1972.285. Two left horn core bases are from Bed I; these are BM(NH) M 14516 found in 1931 and retaining a considerable part of the frontal, and the poorly-preserved M 29421 probably found in 1932.

The overall size of these horn cores might have been a little less than in *P. rugosus*. They are short and thick-set, without mediolateral compression or a flattened lateral surface, curving outwards immediately from the base, then bending backwards and upwards nearer the tips. They are set at a low angle in side view. They tend to have a diagonal-transverse ridge passing across the anteromedial part of the base, and in M 14516 the root of this ridge is so well marked as almost to become a keel recalling that of the cranium 068/5975. The posterior surface is flattened in HWK EE 954 and 2181 and in M 14516. There are also the normal transverse ridges in the middle of the horn cores. They are inserted far behind the orbits, and their pedicels and frontals show extensive sinuses. The dorsal parts of the orbital rims project strongly.

A horn core 1955 P.P.F.4 from the surface of FLK was figured by Leakey (1965 : 65; pl. 88 which is a front view and not a side view as stated in the caption) and tentatively but mistakenly assigned to *Thaleroceros radiciformis*. The horn core is from the left side, and appears to have had a very low insertion angle. It is similar to the horn cores from the HWK sites, but lacks the diagonal-transverse ridge at its base. It remains unidentified.

The *Parmularius rugosus* of Beds III and IV could have descended from *P. angusticornis* by a slight diminution in size, the acquisition of greater outward bending of the horn cores, and a change in the position of the basal swelling of the horn cores. However, the Bed II fossils apparently of *P. rugosus* and the earlier fossils from the HWK area suggest that more probably the lineage was separate. Few changes would be needed to transform the HWK horn cores into *P. rugosus*, and they must represent either its direct ancestor or a racial variant of the lineage which chanced to be in the Olduvai region at that period.

MEASUREMENTS. Measurements on specimens of *P. rugosus* are:

	BM(NH) M 21430	JK2 III TT 1
Anteroposterior diameter at base of horn core	36·8	42·4
Mediolateral diameter at base of horn core	32·3	37·8
Minimum width across lateral surfaces of horn core pedicels	–	*c.* 93·1
Width across lateral edges of supraorbital pits	55·5	–
Length from back of frontals to top of occipital crest	–	*c.* 45·6
Length from back of frontals to back of occipital condyle	–	*c.* 93·0
Length from midfrontal suture at level of supraorbital pits to top of occipital crest	118·4	–
Skull width across mastoids immediately behind external auditory meati	116·3	116·0
Distance from rearmost point of occlusal surface of M^3 to back of occipital condyle	157·0	–
Occipital height from top of foramen magnum to top of occipital crest	39·7	43·9
Width across anterior tuberosities of basioccipital	26·5	32·7
Width across posterior tuberosities of basioccipital	33·5	33·8

Occlusal length M^1–M^3	61·6	–
Occlusal length M^2	22·7	–
Estimated occlusal length P^2–P^4	*c.* 23·2	–

The length of the horn core JK2 III A.03 220 is 228.0, and the basal anteroposterior and lateromedial diameters 47.7 × 36.9 mm.

Measurements on the cranium HWK EE 068/5975 are:

Anteroposterior diameter at base of horn core	39·9
Mediolateral diameter at base of horn core	39·7
Minimum width across lateral surfaces of horn core pedicels	92·4
Occipital height from top of foramen magnum to top of occipital crest	48·7
Width across anterior tuberosities of basioccipital	24·8
Width across posterior tuberosities of basioccipital	30·1

Measurements on the more complete horn cores from the HWK area are:

	HWK EE 2061	HWK EE 2181	HWK EE 954	HWK East 068/6649
Horn core length	215·0	180·0	180·0	–
Anteroposterior diameter at horn core base	50·2	37·6	24·3	30·3
Lateromedial diameter at horn core base	52·9	44·4	31·2	31·0
Minimum width across lateral surfaces of horn core pedicels	96·2	94·6	–	87·2

On HWK EE 2181 the width across the lateral edges of the supraorbital pits is 62·3, and the skull width across the posterior side of the orbits is *c.* 150 mm.

Anteroposterior and mediolateral diameters at the base of the other horn cores in this group are:

HWK II 58	42·7 × 45·0	FLK surface P.P.F.4	47·2 × 48·6
HWK EE II 285 (cast)	37·6 × 44·1	BM(NH) M 14516	40·0 × 49·2

COMPARISONS. Some Elandsfontein horn cores, including a pair SAM 20076, may be assignable to *Parmularius*. They are larger than *P. rugosus* with strong mediolateral compression, inserted uprightly above the orbits on high pedicels and close together, parallel at the base in anterior view, bent sharply backwards in the middle with a pronounced torsion which is clockwise on the right side, and with a swollen base of the medial side and a concavity on the lateral surface. This distinctive and puzzling set of characters leaves little alternative except a doubtful assignment to *Parmularius*.

Genus ***DAMALISCUS*** Sclater & Thomas 1894

TYPE SPECIES. *Damaliscus dorcas* (Pallas 1766).

GENERIC DIAGNOSIS. Medium-sized alcelaphines with high and narrow skulls; horn cores with fairly simple curvature, with transverse ridges, inserted over the back of the orbits, less far back on the skull and less obliquely set than in *Alcelaphus*. Torsion of the horn cores is only incipient and is anticlockwise on the right side. Braincase short but longer than in *Parmularius*; slight tendency to a parietal boss; supraorbital pits set widely apart; preorbital fossae fairly large and larger than in *Parmularius*; moderate to large-sized foramina ovalia; premolar rows fairly long in living species and P_2s often retained.

REMARKS. *Damaliscus* has fewer specialized characters than *Parmularius*. Its tendency to have a parietal boss opens the possibility of a common ancestry with *Parmularius*.

Damaliscus niro (Hopwood 1936)

1936 *Hippotragus niro* Hopwood : 640, no figure.

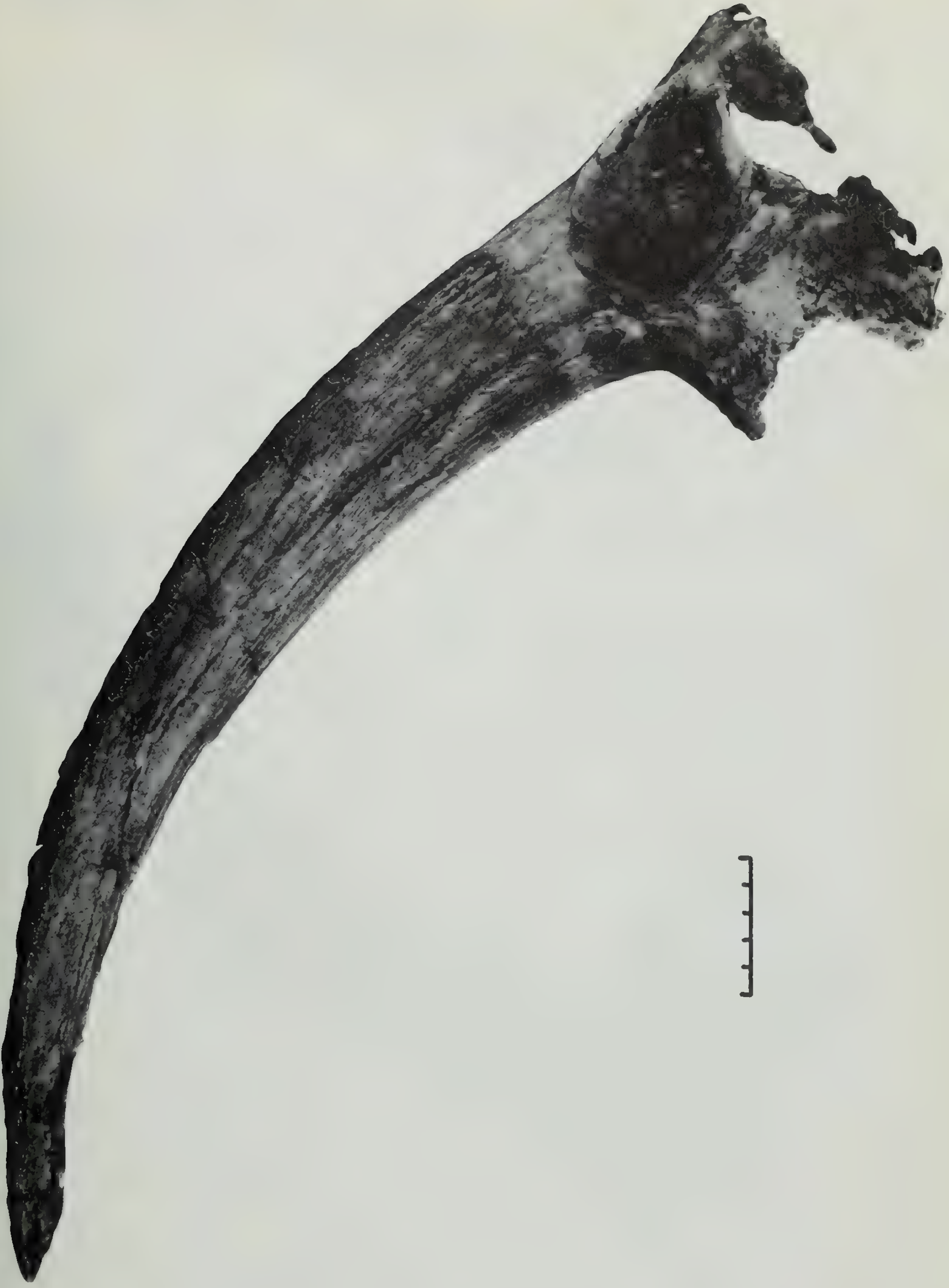


Plate 27 (Scale = 50 mm)

Damaliscus niro. Medial view of cast of left horn core and frontlet from Peninj, BM(NH) M 26546.

1937 *Hippotragus leucophaeus* subsp. Schwarz : 87; pl. 2, fig. 11.
1965 *Hippotragus niro* Leakey : 48; pls 54–55.
1965 *Hippotragus* cf. *niger* Leakey : 50.
1965 *Hippotragus* cf. *equinus* Leakey : 51 (in part).
1965 Other gazelles Leakey : 65(j) (except 473 from HWK II); pl. 86.
1965 Alcelaphini indet. Leakey : 66(e); pl. 92.
1965 *Damaliscus niro* Gentry : 335.

DIAGNOSIS. An alcelaphine about the size of *Damaliscus lunatus* or larger. Horn cores moderately long, strongly compressed mediolaterally especially distally (but less strongly compressed in some Olduvai specimens), frequently with flattened lateral and medial surfaces, the widest part of the cross-section situated anteriorly, inserted above the back of the orbits and obliquely in side view but more uprightly than in *D. lunatus*, divergent as much as in *D. lunatus korrigum* or more so, curved evenly backwards (or in some Olduvai specimens with a fairly abrupt change of course about half way along the horn core length), many examples with strong and widely spaced transverse ridges on the front surface. Horn core pedicels short compared with *Parmularius*; postcornual fossae shallow and rather long; braincase strongly angled on the facial axis; sometimes a slight indication of a parietal boss; orbital rims moderately projecting.

HOLOTYPE. Right horn core BM(NH) M 14561, found in 1931.

HORIZON. The holotype is from JK1 and 2, Bed III (M. D. Leakey 1971b : 283). Other specimens are common in middle Bed II to Bed IV at Olduvai. The species is known from Peninj, and from several sites in South Africa including Cornelia, Florisbad, probably Elandsfontein and possibly Mahemspan.

REMARKS. Specimens of *Damaliscus niro* in London are a left horn core BM(NH) M 29418 found on the surface at SHK II in 1935, left horn core M 21450 found on the surface of BK II in 1935, distal part of a horn core M 21453 which may belong to M 21450, two pieces of horn core M 14564 found in Bed IV in 1931, and part of a horn core M 14519 found in 1931 and said to be from DK I. Part of a horn core M 29417 from the surface of NGC in Bed IV may also be of *D. niro*. M 21450 and M 14564, with the Nairobi horn cores BK II 1953.067/5235 P.P.R.2 and F.971 from the surface of Bed IV in 1941, were recorded as *Hippotragus* cf. *niger* by Leakey (1965 : 50). The piece of a horn core called *Hippotragus leucophaeus* subsp. by Schwarz (1937 : 87; pl. 2, fig. 11) was probably this species. It was lost in Munich during the Second World War, but Schwarz had noted that it was mediolaterally compressed above a thicker lower part.

D. niro was a common antelope in both east and southern Africa. The horn cores in London listed above, and in Nairobi the two horn cores known from SHK II, the right horn core BK II 1955.159, nearly all those in Beds III to IV, and the ones in South Africa all have very strong mediolateral compression and flattened medial and lateral surfaces. The widest part of the cross-section is situated anteriorly, they are curved evenly backwards, and have very marked and widely-spaced transverse ridges on the front surface. This is the morphological pattern found in the holotype. At the BK II site there occur two other horn core varieties which may doubtfully be included in *D. niro*. The first (type A) comprises left horn cores 1952.1495 and 067/5238 (Leakey 1965 : pl. 86, first and third from the left), right 1963.1774, base of right BK II Ext 140, left 1957.876 (Leakey 1965 : pl. 86, fourth from the left), distal end of left BK II Ext 1953.65, and parts of left 1952.254, 1957.49, 1963.067/1594 and BK II Ext 1953.64. A left horn core BK II 1953 (no number), a right tip BK II Ext 1953.139, and part of a right BM(NH) M 29420 of unknown site and horizon are also probably of type A. Type A horn cores have less strong mediolateral compression, flattening of the lateral surface alone, the widest part of the cross-section situated more posteriorly, a more marked change in backward curvature half way between base and tip, a tendency to upturned tips (as occurs in horn cores and especially the horn sheaths of living *D. dorcas* and *D. l. korrigum*), transverse ridges closer together, and a small posterolateral swelling at the base. 1952.1495 and BK II Ext 140 show that the horn core bases are too close to the orbits and the braincase roof is too little angled downwards for satisfactory assignment to *Parmularius*. Two of this sort of horn core also occur at JK2 III, a piece A.976 and part of a

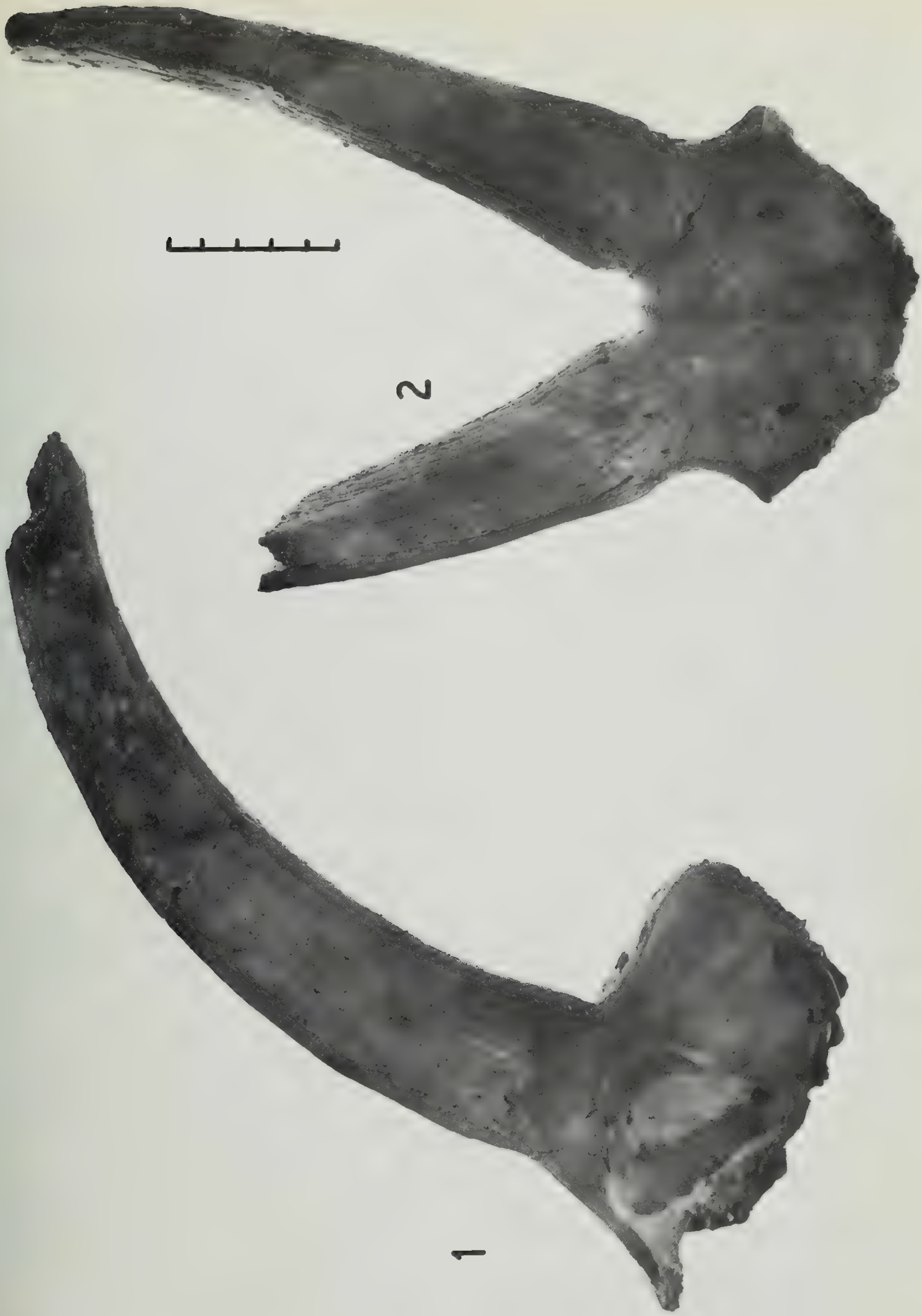


Plate 28 (Scale marked in centimetres)

Fig. 1 ***Damaliscus niro.*** Lateral view of frontlet from Kranskraal near Mazelspoort, Bloemfontein, C.666.

Fig. 2 Anterior view of same.

right A.2348; the last one is more compressed than the Bed II examples. A horn core tip, HWK East II level 2 891, is also like type A but is a little less compressed; we have not assigned it to *D. niro*.

The second group at BK II (type B) comprises the right horn core 067/5237 (Leakey 1965: pl. 86, second from the left), left 1952.252, left 1952.253, left 1953.067/5236 P.P.F.3 (recorded as possibly alcelaphine by Leakey (1965: 66(e); pl. 92)), left BK II Ext 1953.66, left BK II Ext 1953.67, right 1957.365 (taken by Leakey (1965: 51) as *Hippotragus* cf. *equinus*), right 1957.877, left 1963.9, left 1963.408, most of a left 1963.2869 and the horn core base 1963.3043. These also show less mediolateral compression and the widest part of the cross-section situated more posteriorly. However, they have very little or no flattening of the lateral surface, the backward curvature is not so pronounced nor is there a sharp change in course half way along the length of the horn core, transverse ridges are less marked, and there is a swelling of the whole medial surface at the base rather as in *Parmularius angusticornis*.

It is difficult to know how to deal with these horn core varieties which can be assigned to no known alcelaphine other than *D. niro*. Type B could easily be regarded as *D. niro* females of middle Bed II times, and this would require only the reasonable supposition that the three SHK II horn cores are male. If type A horn cores were also females, one would need some additional theorizing. Could they be closer to an ancestral pattern formerly present in both sexes?

The horn cores of *D. niro* differ from those of *D. lunatus* and *D. dorcas* by their mediolateral compression, flattened medial surface, very strong and more widely spaced transverse ridges, smaller increase in divergence from the base upwards, more upright insertions with the appearance of being more directly over the orbits and closer to the supraorbital pits, shallower postcornual fossae, and hollowing of the frontals extending less high above the pedicel top. The lyration of *D. dorcas* horn cores is not found in *D. niro*, and even the greater mediolateral compression of the horn cores of west African populations of *D. lunatus* is exceeded in *D. niro*. Horn cores of the two living species tend to have flattened lateral surfaces (not in *D. l. lunatus*) and the widest transverse diameter lies anteriorly or centrally, so in these two characters they are like *D. niro*. They often have transverse ridges, and these may be more evident distally.

MEASUREMENTS. Anteroposterior and mediolateral basal diameters and lengths of horn cores of *D. niro* are:

SHK II 1953.282	58·8 × 49·4	JK1 and 2 III BM(NH) M 14561	58·1 × 45·7
SHK II surface BM(NH) M 29418	58·6 × 44.1	JK2 III 1963	55·9 × 42·5, length 460·0
BK II 1955.159	67·1 × 51·6	JK2 GP8 III 674	65·7 × 47·8, length 455·0
BK II surface BM(NH) M 21450	56·9 × 43·3	JK2 GP8 III 1627a	61·0 × –, length 485·0
Elephant K II surface 1963.068/5920	65·8 × 49·9		
JK2 III A.1130	57·0 × 48·3		

The width across the lateral edges of the supraorbital pits of JK2 GP8 III 674 is *c.* 61·2 mm.

Anteroposterior and mediolateral basal diameters and lengths of type A horn cores from BK II are:

067/5238	47·8 × 36·4, length 253·0	1963.1774	43·5 × 33·8, length 230·0
1952.1495	50·9 × 39·6, length 335·0	BK II Ext 140	52·0 × 39·6
1957.876	46·0 × 37·2, length 253·0		

Anteroposterior and mediolateral diameters at the base and length of type B horn cores from BK II are:

067/5237	46·9 × 36·4	1957.877	length 345·0
1952.252	49·7 × 39·4, length 335·0	1963.9	49·7 × 38·9, length 315·0.
1957.365	52·3 × 41·6		

COMPARISONS. *D. niro* occurs at Peninj, and it was on a very large left horn core with part of the cranium attached from that site, A67.229 (WN64.174.CFG III.MZ), that the generic identity was established (Gentry 1965 : 335). The Peninj specimen (Pl. 27) has less extreme flattening of the medial and lateral surfaces of the horn core than in the most 'advanced' ones at Olduvai. This helps to link these horn cores with type B horn cores at BK II. The parietal is sufficiently preserved to be fairly certain that there was no boss or tuberosity in its centre.

Measurements on this horn core are:

Anteroposterior diameter of horn core at its base	64·2
Mediolateral diameter of horn core at its base	50·9
Width across lateral edges of supraorbital pits	62·9

A cast of the Peninj specimen is in London, BM(NH) M 26546; the horn core tip is not present on the fossil but has been artificially restored on the cast. A right horn core base with the mid-frontal suture and part of the orbit, A67.236 (WN63.390), also represents *D. niro* at Peninj. Its anteroposterior and mediolateral diameters are 63.9 and 51.3 mm. A horn core base A67.231 (WN64.239.JHG? ?USC) may be of this species.

There is good representation of *D. niro* in South Africa. The most complete specimen is a cranium with the left and part of the right horn core C.666 from the Modder River, Kranskraal 134, near Mazelspoort, Bloemfontein district, in the National Museum, Bloemfontein (Pl. 28). It shows the horn cores to be strongly compressed above the basal part, inserted above the orbits and with flattened medial and lateral surfaces, the braincase bent on the facial axis, a small forward indentation centrally in the parietofrontals suture, small supraorbital pits which are wide apart, frontals raised between the horn core bases, and a parietal boss developed about as much as in living *Damaliscus* and therefore a lot less than in *Parmularius altidens*.

Measurements on the Kranskraal cranium C.666 are:

Anteroposterior diameter of horn core at its base	47·5
Mediolateral diameter of horn core at its base	43·3
Minimum width across lateral surfaces of horn core pedicels	96·4
Width across lateral edges of supraorbital pits	56·0
Maximum braincase width	73·3

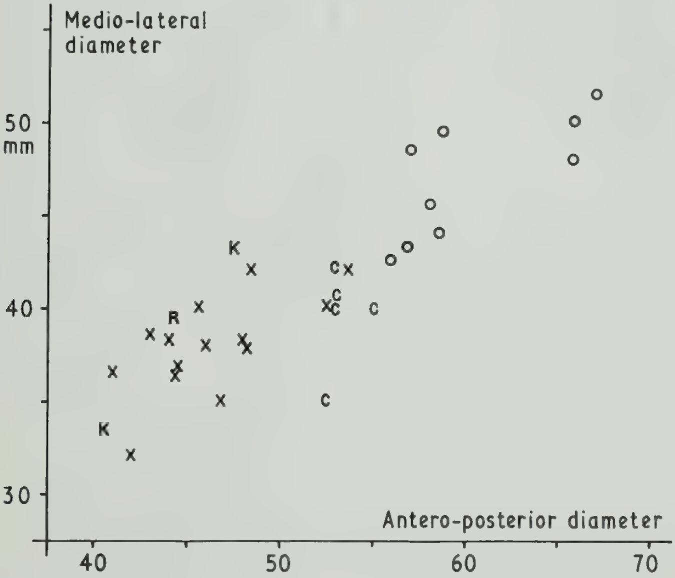
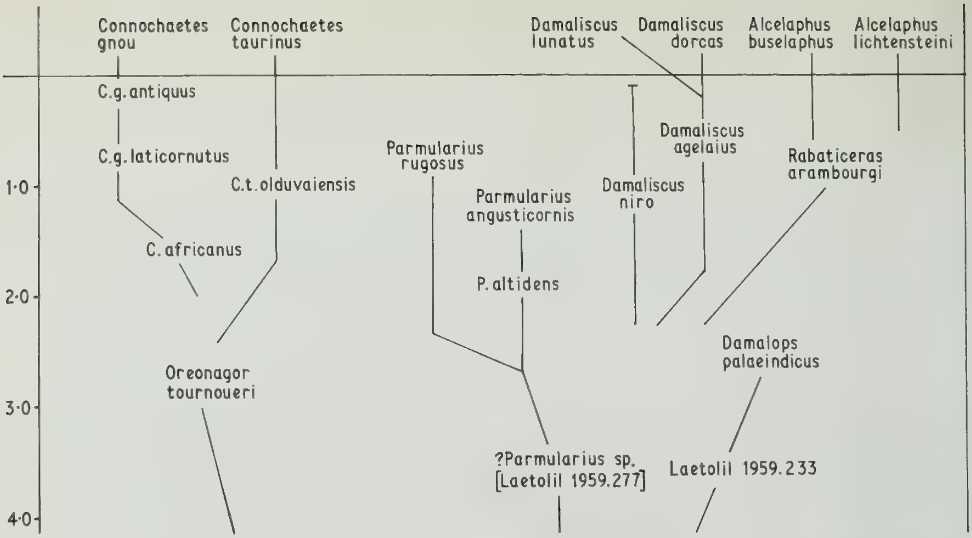


Fig. 27 Basal horn core dimensions of *Damaliscus niro*.
O = Olduvai Gorge, C = Cornelia, X = Florisbad, K = Kranskraal, R = Rustfontein.
There appears to be a size diminution in the later part of the species' temporal range.



Connochaetes gnou
Connochaetes taurinus
Damaliscus lunatus
Damaliscus dorcas
Alcelaphus buselaphus
Alcelaphus lichtensteini
C.g.antiquus
C.g.laticornutus
C.t.olduvaiensis
C.africanus
Oreonagor tournoueri
Parmularius rugosus
Parmularius angusticornis
P.altidens
?Parmularius sp. [Laetolil 1959.277]
Damaliscus agelaius
Damaliscus niro
Rabaticeras arambourgi
Damalops palaeindicus
Laetolil 1959.233
1·0
2·0
3·0
4·0

Fig. 28 Suggested phylogeny for alcelaphines of the *Connochaetes*, *Parmularius* and *Alcelaphus*/*Damaliscus* groups. Living species are shown above the horizontal line, and age is shown on the left in millions of years.

There is also a horn core C.643 from Kranskraal, 12 horn cores from Florisbad (all numbered C.1457), six from Cornelia (five numbered C.770 and one C.2864), three from Rustfontein (C.2756, C.2757 and C.2758), one from Vlakkraal (C.1542), some doubtful horn cores and small mandibles from Mahemspan, and possibly two horn cores from Elandsfontein (8560 and 20043). The horn from the Wonderwerk Cave described by Wells (1943 : 268) as cf. *Capra walie* belongs to *D. niro*. Wells (1970) also reports *D. niro* from Driefontein in the Cape Province. The Florisbad horn cores are smaller than those from Cornelia, and even the latter are smaller than the very large East African specimen from Peninj (Fig. 27). None show the abrupt bending back in mid course seen in many of the Olduvai Bed II horn cores assigned to *D. niro*. It is interesting that only two possible horn cores of this species are known from Elandsfontein.

Since the size diminishes in passing from Cornelia to Florisbad one wonders whether the species recently became extinct or whether it was transformed into *D. dorcas*. The former seems more likely on the present insubstantial evidence. A left horn core C.2930 from Florisbad has been noticed by Wells & Cooke (ms.) as possibly the blesbok, and we found two very similar horn cores in Cape Town, also from Florisbad, a right 3462 and a left 3464. Neither the inclination nor divergence of insertions can be assessed on these horn cores. They are larger than *D. niro* at the same site, the medial surface is more rounded and the whole horn core less compressed mediolaterally, the widest part of the transverse section is less anteriorly placed, and they have a slight alteration in course (lyration) seen in anterior view near the base. They differ from *D. dorcas* in their larger size, less mediolateral compression, and in the lyration lying nearer to the base, but are entirely suitable as ancestors. From Vlakkraal there are a left and two right horn cores (all numbered C.1540) of the Florisbad species like *D. dorcas* and a right horn core (C.1542) of *D. niro*. The three former are smaller than the Florisbad examples, and show more oblique insertions than *D. niro* and a high-extended hollowing in the pedicel. Horn cores of the living *D. lunatus lunatus* have little or no mediolateral compression and no flattening of the lateral surface. Perhaps they share with *D. dorcas* and the Florisbad horn cores C.2930, 3462 and 3464 a descent from *D. agelaius* (p. 402), and neither comes from the longer-separated lineage of *D. niro*. However, this is a tentative hypothesis and it is unfortunate that there is not a single complete tooth row known to be of *D. niro* from any African site.

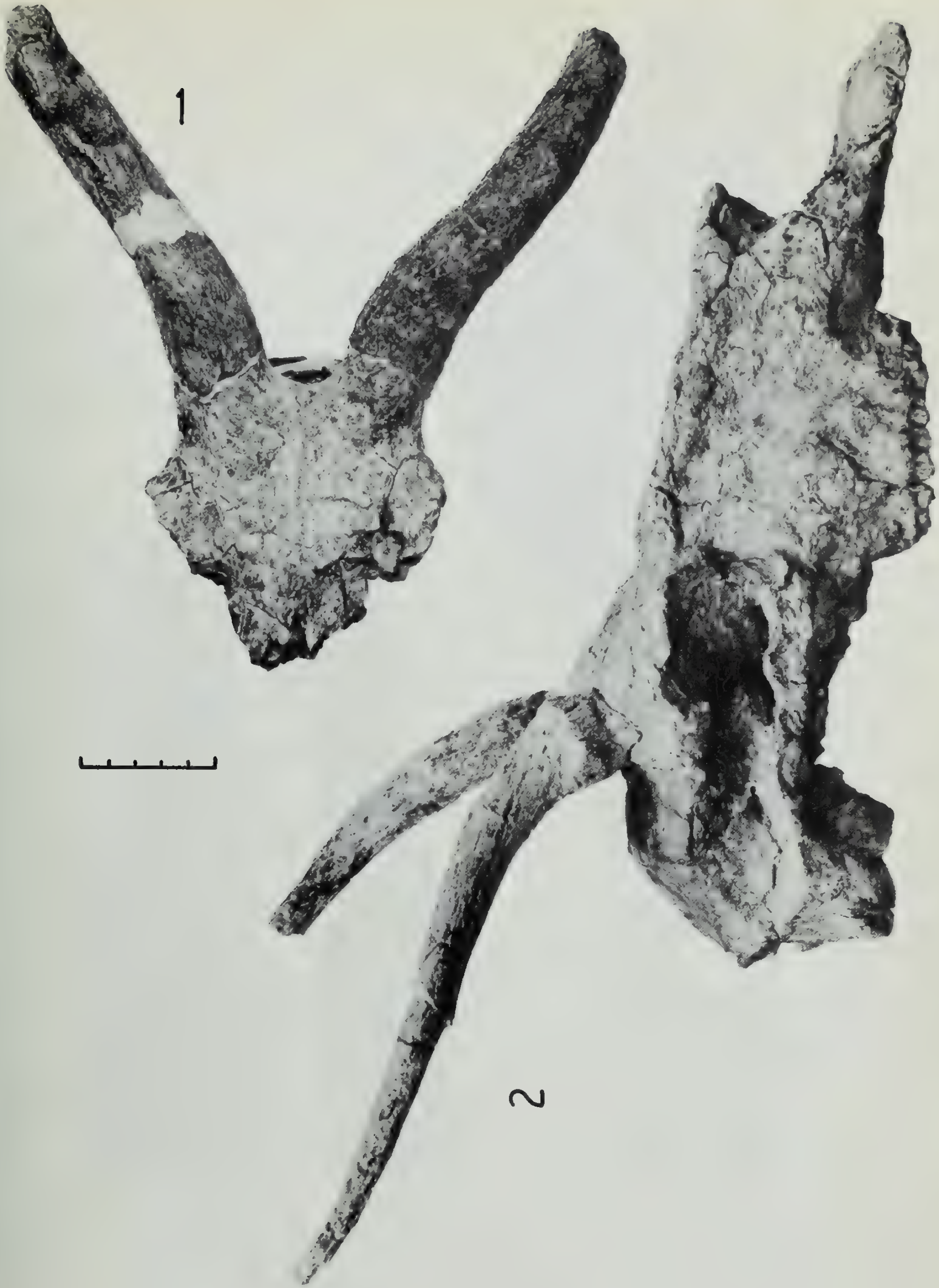


Plate 29 (Scale = 50 mm)

Damaliscus agelaius

Fig. 1 Anterior view of male cranium, VFK III–IV 214.

Fig. 2 Lateral view of holotype female skull, VFK III–IV 350.

The horn cores of the Laetolil cranium 1959.277, already mentioned in the account of *Parmularius altidens*, have some features in common with the type A horn cores of *Damaliscus niro* from BK II. They are a little compressed mediolaterally, the widest part of the cross-section is not situated anteriorly, there is a marked change in backward curvature just over half way between base and tip and a posterolateral swelling at the base. They differ in the absence of transverse ridges or clear flattening of the lateral surface, and more interestingly in the presence of a higher horn core pedicel. A horn core L.292-29 from member C of the Shungura Formation has some similar features to the Laetolil fossil and to *D. niro* type A horn cores. It is somewhat damaged at the base, but shows very slight mediolateral compression, the widest part of the transverse section not situated anteriorly, marked backward curvature near its middle, transverse ridges and an upturned tip. The lateral surface appears not to have been flattened. The parietal boss of the Laetolil cranium is also a resemblance to the *Damaliscus niro* partial cranium shown in Plate 28. There is little use in pursuing this discussion any further because of the uncertain identity of the BK II type A horn cores, and our ignorance of so much of the cranial morphology of *D. niro*. We can conclude only that 1959.277 points to the possibility of an immediate common ancestry for *Parmularius* and *Damaliscus niro* (but see also p. 412). A tentative phylogeny is shown in Fig. 28.

Damaliscus agelaius sp. nov.

Diagnosis. A species of *Damaliscus* smaller than *D. lunatus* and about the size of *D. dorcas*; horn cores smaller than in *D. dorcas*, moderately long and little compressed, inserted closer together and more uprightly than in living *Damaliscus*, in the males diverging to an extent intermediate between *D. lunatus lunatus* and *D. l. korrigum* and in the females less divergent, a few with transverse ridges but none with flattening of the medial or lateral surfaces. Frontals less convex in front of the horn core bases than in living *Damaliscus* and less uparched between the horn core bases than in *D. dorcas*; braincase longer than in living *Damaliscus*; no indication of a parietal boss; supraorbital pits as wide apart as in the living species; no ethmoidal fissures; deeper preorbital fossae than in *D. dorcas*; basioccipital rather short; auditory bullae more inflated than in *D. dorcas*; occlusal complexity of cheek teeth less than in living *Damaliscus*; premolar rows shorter than in living *Damaliscus*; P_2s absent.

Holotype. Female skull 350 with complete horn cores, maxillae and associated mandibles excavated from Fifth Fault Korongo (site VFK) in 1962 (Pl. 29, fig. 2). It is in the National Museum of Kenya, Nairobi.

Horizon. The holotype and other members of a fossilized herd of which it was a member came from Beds III–IV in an area of the Gorge where these Beds are not divisible (M. D. Leakey 1971b : 282). A few other specimens come from Beds II to III–IV.

Remarks. This species is noteworthy for possessing so few specialized characters. The specific name is taken from the Greek ἀγελαῖος (agelaios), with the meaning 'belonging to a herd'. The herd in question was found embedded in a clay matrix (Leakey 1965 : 107). Most of the skulls are complete but rather crushed, often in a transverse plane. There are about 16 skulls of which one, a cranium 214 (Pl. 29, fig. 1), is male. The horn cores have moderately long pedicels and are inserted fairly close together and above the back of the orbits. The suture of the parietofrontals has no central anteriorly-directed indentation. Skull characters which are typically alcelaphine are the anterior thickening of the zygomatic arch, the position of the infraorbital foramen, shape of the mastoid exposure, the median indentation at the back of the palate passing to a level just anterior to the lateral ones, the long nasals, the premaxillae having an even width and contacting the nasals, the occipital surface in two planes with a median vertical ridge, and the basioccipital with a central longitudinal groove and no constriction across its centre.

A male cranium with incomplete horn cores, S.38, was found *in situ* at geologic locality 54 in 1968 (Pl. 25, fig. 1). That it is almost certainly from Bed II above the Lemuta Member is shown by the relatively high augite content and a small number of altered fragments of mafic volcanic glass in the matrix (R. L. Hay, personal communication, September 1973). It is not at all crushed and shows without doubt that this species had a longer braincase than living *Damaliscus*.

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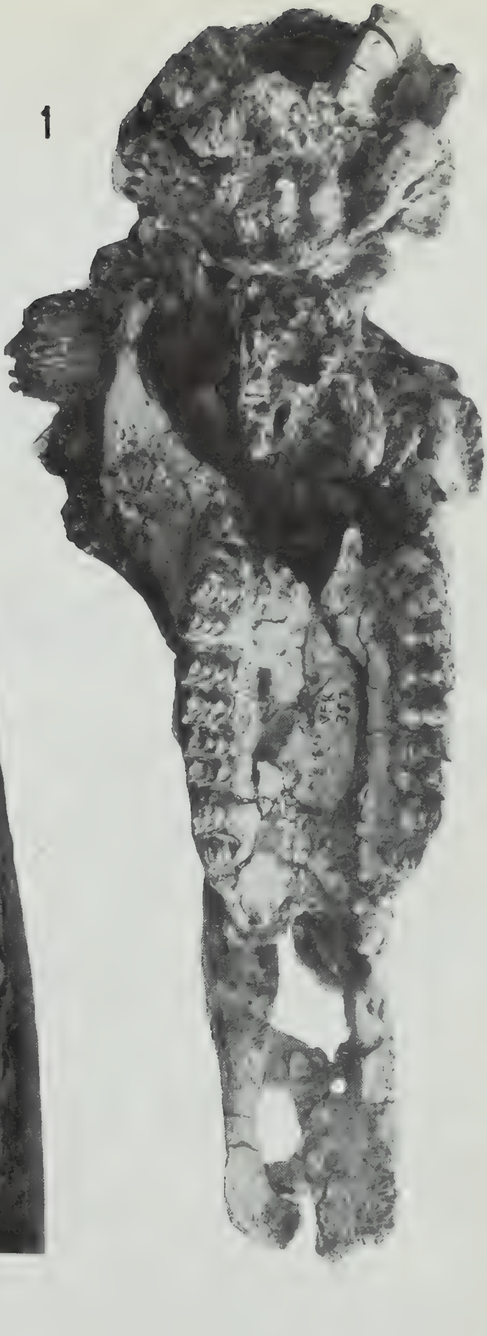

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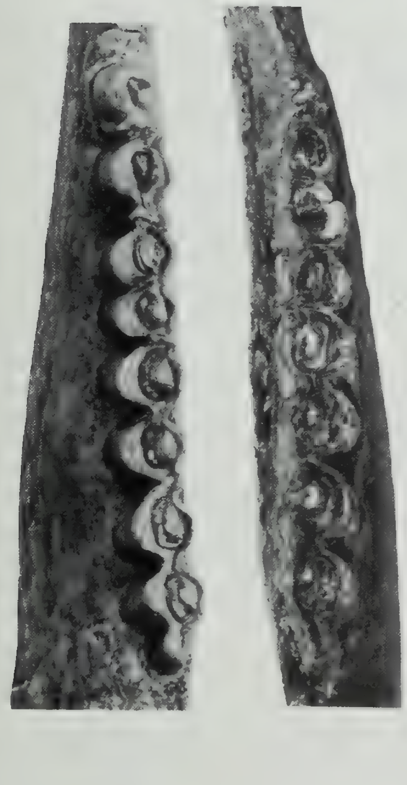

Plate 30 (Scale = 50 mm for skull and 25 mm for teeth)

Fig. 1 ***Damaliscus agelaius.*** Palatal view of skull, VFK III–IV 357.

Fig. 2 Lower left dentition of ***Damaliscus agelaius*** VFK III–IV 363 (left) compared with lower right dentition of ***Parmularius altidens*** FLKN I 1109 (right).

FLKW 1969.82a is an alcelaphine skeleton with the skull represented by a crushed cranium with horn cores. It was found above Tuff IF in greenish clays below the Sandy Conglomerate west of FLK. Some antilopine limb bones were found in association, for example a right metatarsal and a proximal right tibia. The skull is about the same size or even marginally larger than those of the VFK herd. It appears to be *D. agelaius* in its relatively small horn cores, their upright insertions above the backs of the orbits, the length and inclination of the braincase roof, and there being scarcely any sign of a parietal boss. The femur is rather short. The crushing forbids the assessment of further characters. This skull and skeleton is the earliest known representative of the species.

Other specimens are a left horn core A.1446 found in 1962, a partial horn core marked '1961 B.T.T.F. Floor', both female, and probably a distal half of a horn core A.345, all from JK2 III. In addition there is a right horn core with the frontal suture and orbital rim 068/6661 found on the surface at Hoopoe Gully in 1962 which has the robustness and divergence appropriate for a male of this species, and a male frontlet 068/5730 found in 1961 and labelled XDK. According to R. L. Hay (personal communication, September 1973) matrix from inside the horn core of 068/6661 was a light olive-grey claystone, locally sandy, and quartzose sand. Outside was a calcareous quartzose sandstone. The horn core is most likely to have originated from Beds III–IV (undivided), but Bed II cannot be excluded. The matrix of 068/5730 was a quartzose sandy limestone, and depending on provenance could be from Beds II, III, III–IV (undivided) or IV.

Damaliscus agelaius differs from its contemporary *Parmularius rugosus* in having horn cores inserted more uprightly in side view and less posteriorly on the skull, a longer braincase, less of a parietal boss, larger preorbital fossae, smaller teeth relative to the size of the skull, and less shortened premolar rows (Fig. 29). The species is smaller than *Damaliscus niro* and is without that

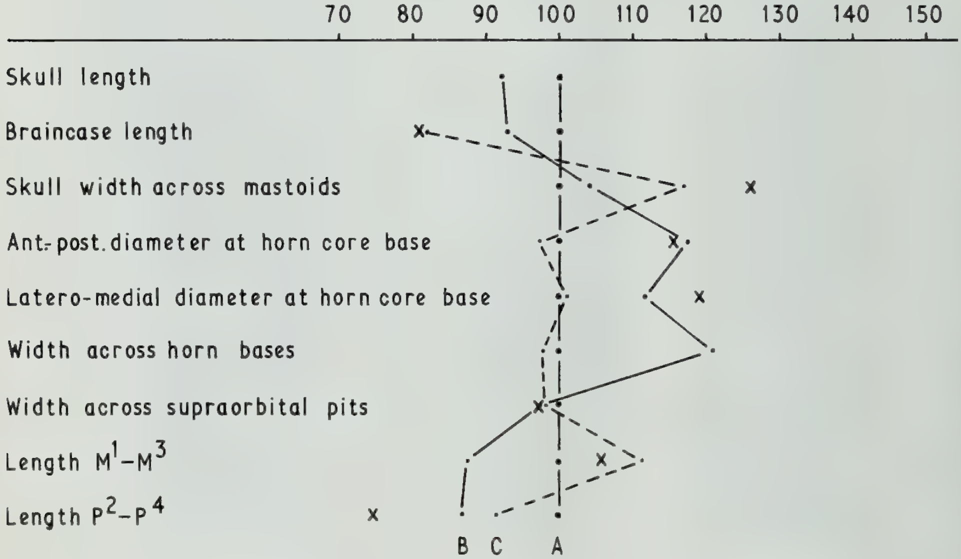

Fig. 29 Percentage diagram of some skull measurements in some alcelaphines.

A = standard line at 100% for mean of females in the Olduvai herd of *Damaliscus agelaius*.

B = mean for three female *D. dorcas dorcas* (except that the two horn core diameters are from a female *D. d. phillipsi*).

C = *Parmularius altidens* holotype.

Crosses = *P. rugosus* holotype.

Braincase length is measured from the back of the frontals to the occipital top. Compared with *D. agelaius*, *D. dorcas* has evolved a shorter braincase and larger, more compressed horn cores set wider apart. *Parmularius* species show a shorter braincase and a short premolar row.

species' distinctive characters of mediolaterally compressed horn cores with flattened medial and lateral surfaces and strong and widely spaced transverse ridges. On the whole the dentitions of *D. agelaius* are smaller than those presumed to belong to *D. niro*, although the ranges of the two species overlap. *D. agelaius* is a more likely ancestor for *D. lunatus* than is *D. niro*, and may be ancestral to *D. dorcas* as well. However, all the mandibles of *D. agelaius* lack an alveolus in the jaw for a P_2 and this may preclude it from ancestry to living *Damaliscus*. P_2 is still customarily present in *D. lunatus*, while in a sample of *D. dorcas* 18 individuals have P_2 and 11 do not. R. G. Klein, who supplied information on *D. dorcas* from the collections of the South African Museum, believes that P_2s tend to be lost with increasing ontogenetic age.

Measurements. Measurements on the more complete skulls of the VFK III–IV herd and the cranium S.38 from geologic locality 54, Bed II, of *D. agelaius* are:

	350	150	235	363	214	S.38
	♀	♀	♀	♀	♂	♂
Skull length from front of the premaxillae to back of the occipital condyles	347·0	–	–	319·0	–	–
Skull width across posterior side of orbits	–	126·5	–	–	–	119·0
Length of horn core along its front edge	247·0	–	235·0	–	–	–
Anteroposterior diameter of horn core at its base	30·2	–	29·2	31·4	39·2	–
Mediolateral diameter of horn core at its base	24·4	–	24·4	–	36·9	36·9
Minimum width across lateral surfaces of horn core pedicels	68·3	–	75·3	–	93·2	86·1
Width across lateral edges of supraorbital pits	–	–	60·0	–	67·0	68·8
Length from back of frontals to top of occiput	–	64·5	–	–	–	–
Maximum braincase width	–	72·8	–	–	75·0	75·3
Skull width at mastoids immediately behind external auditory meati	91·6	98·3	–	90·5	–	94·0
Occipital height from top of foramen magnum to top of occipital crest	–	34·3	–	34·3	–	–
Width of anterior tuberosities of basioccipital	–	25·7	23·5	–	–	–
Width of posterior tuberosities of basioccipital	–	–	35·5	–	–	–
Occlusal length M^1–M^3	56·8	58·1	57·1	55·9	–	–
Occlusal length M^2	18·9	22·1	21·8	20·2	–	–
Occlusal length P^2–P^4	28·9	35·5	31·6	30·5	–	–
Occlusal length M_1–M_3	58·1	–	–	59·7	–	–
Occlusal length M_2	19·2	–	–	19·4	–	–
Occlusal length P_3–P_4	21·5	–	–	23·1	–	–

Measurements on 16 female horn cores of *D. agelaius*, including four from the skulls whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length of horn core along its front edge	6	236·0	220·0–266·0	22·0	9·10
Anteroposterior diameter of horn core at its base	15	31·8	29·2–39·2	1·8	0·49
Mediolateral diameter of horn core at its base	15	27·1	23·6–36·9	2·6	0·76
Minimum width across lateral surfaces of horn core pedicels	7	73·9	68·3–93·2	4·4	1·97

The JK2 III–IV horn cores are not measurable. The anteroposterior and mediolateral basal diameters of 1962.068/6661 from Hoopoe Gully are 35·7 × 29·9 mm.

Measurements on 15 maxillae of *D. agelaius*, including four from the skulls whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M^1–M^3	14	58·2	55·0–62·3	2·1	0·57
Occlusal length M^2	14	20·8	18·9–22·5	1·1	0·29
Occlusal length P^2–P^4	10	31·0	29·2–35·3	1·9	0·61

Measurements on six mandibles of *D. agelaius*, including two from the skulls whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_1–M_3	5	61·8	58·1–65·1	3·0	1·35
Occlusal length M_2	6	20·0	19·2–21·4	0·8	0·32
Occlusal length P_3–P_4	5	22·4	21·5–23·4	0·8	0·36

Measurements on the skull of FLKW 1969.82a are:

Anteroposterior diameter of horn core at its base	*c.* 35·0
Length from back of frontals to top of occiput	*c.* 80.0
Width of anterior tuberosities of basioccipital	24·5
Width of posterior tuberosities of basioccipital	*c.* 34·0
Occlusal length M_1–M_3	*c.* 62·0
Occlusal length M_2	19·3
Occlusal length M_3	26·0
Occlusal length P_3–P_4	*c.* 25·2
Occlusal length P_4	14·4

It is not clear whether or not P_2 was present in life.

Lengths and least thicknesses of the associated limb bones are:

Left femur	95	242 × 23·2	Left metatarsal	96	246 × 17·9
Left tibia	94	306 × 24·7	Left metacarpal	100	234 × 19·9

Comparisons. An alcelaphine about the size of *Damaliscus dorcas* or a little larger, from the Pinjor Formation of the Siwalik Hills, was referred by Pilgrim (1939 : 67) to *Damalops palaeindicus* (Falconer). The Pinjor Formation may be between two and three million years old by faunal correlation (Maglio 1973 : 70–71). Specimens in London are a damaged adult skull BM(NH) 39594, an immature skull 39598 figured by Lydekker (1886 : pl. 4, figs 3, 3a), an isolated right horn core thought to be from the same block of matrix as 39594, and a palate and paired mandibles 39571. In this species the slender horn cores are inserted fairly uprightly, they curve slightly backwards and have increasing divergence towards the tips, the cross-sectional long axis of the horn cores is set at an angle rather than nearly parallel to the long axis of the skull, the preorbital fossae are large and deep, the braincase is moderately angled on the facial axis, the premolar row is fairly long (a little less so than in living *Alcelaphus* and *Damaliscus*), P_2 is present, and P_4 has a fused paraconid and metaconid. The immature skull 39598 and Lydekker's illustration (1886 : pl. 4, fig. 5) of the holotype skull in Calcutta show that there is no parietal boss in this species. With the course of its horn cores, large preorbital fossae and the presence of P_2, *Damalops palaeindicus* may be related to the *Damaliscus–Alcelaphus* group. *Damaliscus agelaius* differs from it in its more upright horn core insertions, the longitudinal cross-section of the horn cores being more nearly parallel to the longitudinal axis of the skull, a less sloping dorsal part of the orbital rim, the braincase roof being perhaps less slanted, and a shorter premolar row arising mostly from the absence of P_2. It also existed in a later time span than *Damalops palaeindicus*.

Genus ***RABATICERAS*** Ennouchi 1953

1953 *Rabaticeras* Ennouchi : 126.

Type species. *Rabaticeras arambourgi* Ennouchi.

Generic diagnosis. As for the single species.

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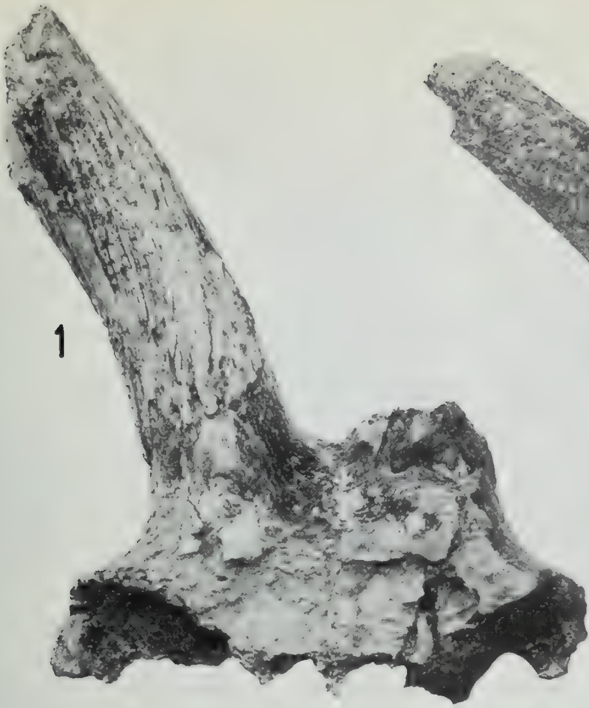

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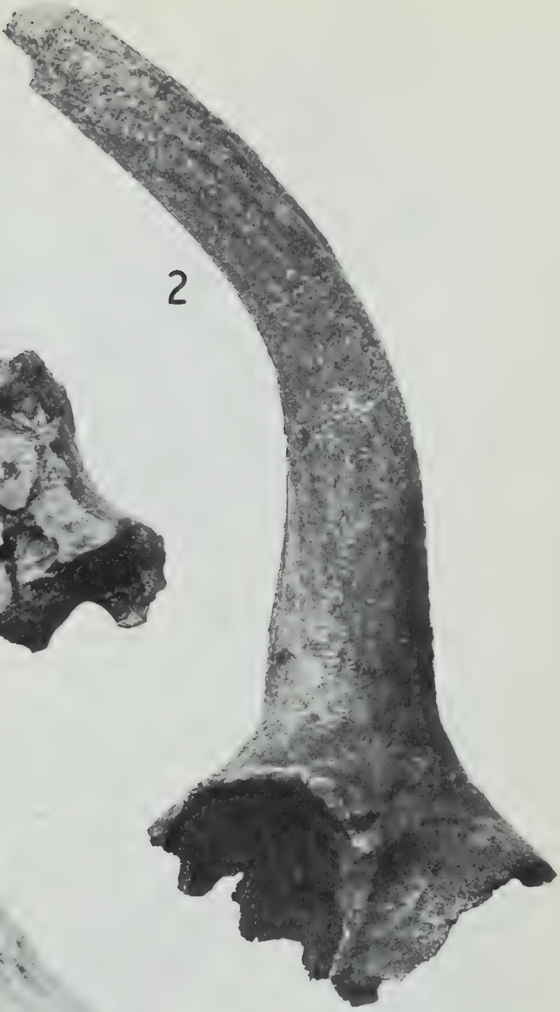

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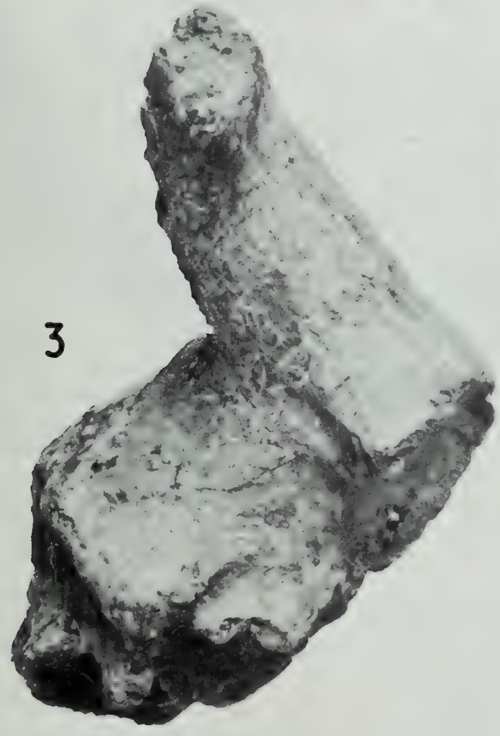

Plate 31 (Scale = 50 mm)

Fig. 1 ***Rabaticeras arambourgi.*** Anterior view of frontlet, JK2 III A.1129.

Fig. 2 ***Rabaticeras arambourgi.*** Lateral view of left horn core, JK2 III B.E/S K7-1.

Fig. 3 **Alcelaphini** sp. 2. Lateral view of cranium S.208 from Lemuta Tuff Member, lower Bed II.

Rabaticeras arambourgi Ennouchi 1953

1953 *Rabaticeras arambourgi* Ennouchi : 126, figs 1–2.

DIAGNOSIS. An alcelaphine with skull proportions nearer to high and narrow than to low and wide; horn cores moderately long, mediolaterally compressed, sometimes with a flattened lateral surface at least near the base and an approach to a posterolateral keel, inserted close together and above the back of the orbits, little divergent at the base but increasingly so in the middle part and then reapproaching at the tips, twisted in a clockwise direction in the right horn core[4], inserted quite uprightly in side view and curving forwards towards the tips; braincase strongly angled on the facial axis and with parallel sides. Frontals between the horn core bases at a higher level than the dorsal parts of the orbital rims; no parietal boss; moderately projecting orbital rims; occipital surface almost in one backward-facing plane with a slight vertical ridge and no hollows on either side; foramina ovalia small to moderate-sized.

HOLOTYPE. A frontlet with the basal halves of both horn cores, collected in 1951, number 29 in Rabat.

HORIZON. The holotype came from a sandstone in Quarry 8 on the coastal road from Rabat to Témara, Morocco, and further conspecific pieces from overlying red clays at Bou Knadel, 20 km north of Quarry 8. These occurrences might range as late as Soltanian in age, so that Middle–Upper Pleistocene is a possible age for *R. arambourgi* in Morocco. Details of Moroccan geological and climatic successions are given in Biberson (1967 : 361; 1971) but the level of *R. arambourgi* has not been established. The main difficulty arises from the frequent use of the expression 'the Rabat sandstone' in the literature, since there are a number of sandstones at Rabat ranging from lower to terminal Pleistocene (Biberson, personal communication).

Remains inseparable from the holotype come from Bed III and probably Bed IV at Olduvai and it is common at Elandsfontein. A similar animal comes from Bed II at Olduvai (see p. 417), and a further one from Swartkrans.

REMARKS. The best two Olduvai specimens of this species are from JK2 in Bed III. These are a frontlet A.1129 with both orbital rims and the proximal half of the right horn core, and an almost complete left horn core B.E/S K7-1 with the frontal, parietal, complete orbital rim and supraorbital pit (Pl. 31, figs 1, 2). The mid-frontal and parietofrontal sutures are not very complicated, and there is no indentation in the middle of the parietofrontal suture. A fragmentary left horn core A.346 may be the same species. It is also probable that a left horn core with part of the frontal PDK IV 1970.1498 belongs to *R. arambourgi*. The Olduvai material cannot be distinguished from the Moroccan species. A specimen from Morocco was given to the Institut de Paléontologie in Paris by M. Ennouchi and a cast of this fossil was kindly sent to us by Mlle Signeux and is now in the British Museum (Natural History), M 31901. It is a frontlet with complete left horn core, frontals with supraorbital pits and a small part of the braincase roof, and seems to be smaller than the holotype. It is about the size of a hartebeest and the horn core is moderately long and mediolaterally compressed with a flattened lateral surface and approach to a posterolateral keel, twisted in an anticlockwise direction, inserted rather uprightly, close to the midline and above the back of the orbits, little divergent at the base but increasing in the middle part and then reapproaching at the tip. The braincase is strongly angled on the facial axis and the frontals between the horn core bases are higher than the top of the orbital rims. Since the horn cores of *Rabaticeras* are inserted more anteriorly than in *Parmularius*, there can be no doubt that the steep angle of the braincase roof in profile must be linked with reorientation of the brain cavity internally.

Ennouchi thought that his new frontlet was a caprine. However, both the Olduvai frontlet and Elandsfontein specimens show that the horn cores are not hollowed, there are no caprine teeth at either Olduvai or Elandsfontein, and the basioccipital on an Elandsfontein cranium is typically

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[4] Following the observations of Vrba (1971 : 62), we would like to extend the list of Gentry (1970a : 274) of bovids in which torsion of the horn cores is clockwise on the right side to comprise *Menelikia*, *Megalotragus*, *Connochaetes*, *Oreonagor*, *Alcelaphus*, *Rabaticeras*, *Antidorcas*, *Sinotragus*, *Ovibos*, *Parurmiatherium*, *Bootherium*, *Euceratherium*, *Benicerus*, *Oioceros*, *Sivacapra*, most *Ovis* and some Bovini.

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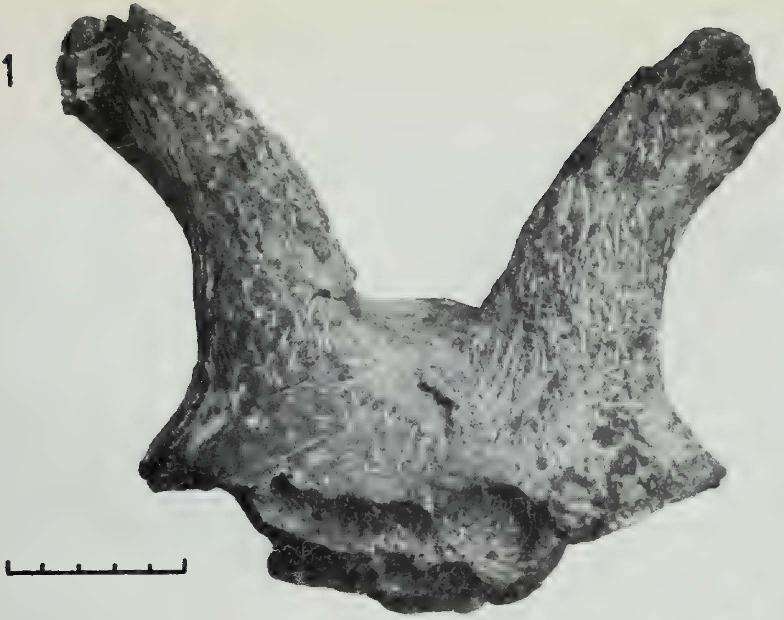

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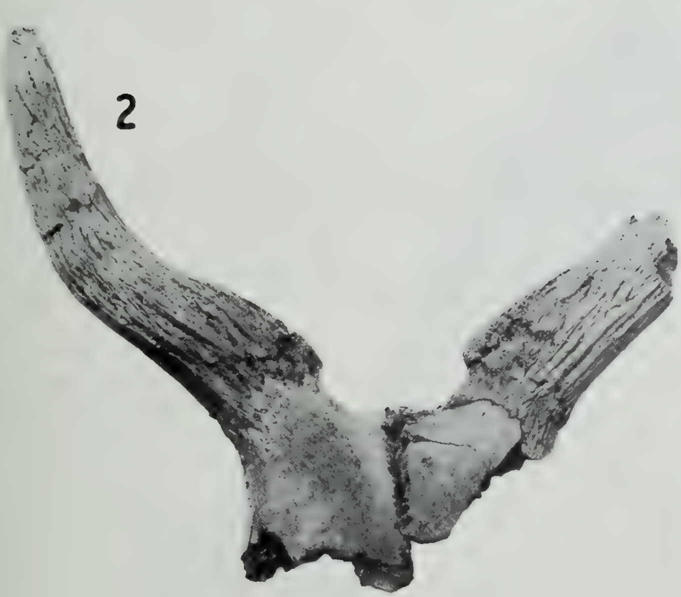

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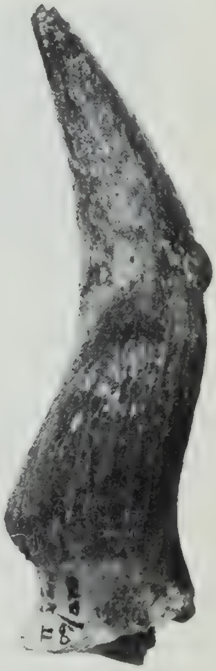


Plate 32 (Scale = 50 mm)

Fig. 1 **Alcelaphini** sp. 2. Anterior view of cranium S.208 from Lemuta Tuff Member, lower Bed II.

Fig. 2 ***Parmularius*** aff. ***rugosus.*** Anterior view of immature frontlet, HWK East 1962.068/6649 from middle Bed II.

Fig. 3 ***Parmularius*** aff. ***rugosus.*** Anterior view of left horn core, HWK 1960.58 from lower Bed II.

alcelaphine and unlike caprines in its central longitudinal groove and anterior tuberosities about as wide instead of wider than the posterior ones. The tendency to a posterolateral keel can be matched among caprines only in *Capra falconeri*, the horn cores of which do not otherwise resemble *R. arambourgi*.

R. arambourgi is a good candidate for the ancestry of the living hartebeest *Alcelaphus buselaphus*. The fossil horn cores differ from the South African *A. buselaphus caama* only in their more upright insertions, less divergence, less abrupt alterations in course (in particular the lack of a sharp backward bend at the tips) and the absence of the long united pedicel. Also the braincase has parallel sides instead of widening posteriorly. The evolution of the united pedicel and the sharper curvature of the horn cores of *A. buselaphus* must have taken place very rapidly since Olduvai Bed III and Elandsfontein times. Similarly fast evolution has already been postulated for *Connochaetes gnou* (p. 365). It is interesting that the three localities for *Rabaticeras* are within the wide geographical range of living or recently exterminated *A. buselaphus* populations. It is apparent from the dating of the Olduvai beds that if *Rabaticeras* is ancestral to *Alcelaphus*, then this lineage is unlikely to have split from *Damaliscus* less than one million years ago. This is interesting in relation to the recorded hybridization between living species of *Damaliscus* and *Alcelaphus*. If further finds substantiate the connection between *Rabaticeras* and *Alcelaphus*, it would become appropriate to abandon *Rabaticeras* as a separate genus.

MEASUREMENTS. Measurements on the two Bed III specimens of *R. arambourgi* and the frontlet in Paris are:

	JK2 A.1129	JK2 B.E/S K7–1	Paris
Skull width across posterior side of orbits	152·0	–	–
Anteroposterior diameter at horn core base	47·5	47·0	*c.* 42·0
Lateromedial diameter at horn core base	41·4	39·5	*c.* 32·0
Minimum width across lateral surfaces of horn core pedicels	99·4	–	84·0
Width across lateral edges of supraorbital pits	70·8	–	58·3

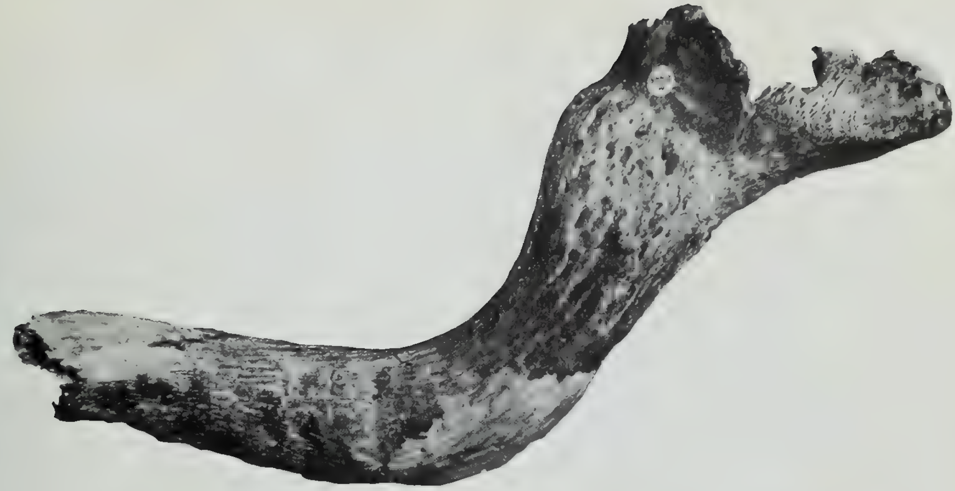
The horn core PDK IV 1498 has anteroposterior and lateromedial basal diameters of 37·1 and *c.* 34 mm.

COMPARISONS. *Rabaticeras arambourgi* is a very common antelope at Elandsfontein. Its remains include a cranium with the bases of both horn cores 9470, a complete right horn core with the frontal 4498, a number of frontlets and many horn cores. The cranium has a narrow and strongly angled braincase with an alcelaphine-like basioccipital. The Elandsfontein material appears to be from a slightly smaller animal than at Olduvai, and the measurements of the Moroccan specimen fall within the Elandsfontein range.

Vrba (1971) has described from Swartkrans, South Africa, an antelope frontlet like *R. arambourgi* but larger and with proportionally smaller horn cores. She believed it to be a new species and thought at that time that it could best be referred to *Damaliscus*. Accordingly she proposed the name *Damaliscus porrocornutus* for the Swartkrans species. We may expect the future discovery of a greater range of infraspecific and supraspecific regional variation in *Rabaticeras*.

Alcelaphus buselaphus is known from late north-west African sites. Arambourg (1938 : 37) considered that Pomel's names *Boselaphus probubalis*, *B. saldensis* and *B. ambiguus* were all referable to this species. The shape of the horn cores on a frontlet of *B. probubalis* from Aboukir, Algeria (Pomel 1894 : pl. 4, figs 14–15), suggest in their anterior aspect that they could be from an ancestor of the extinct north African race, *A. buselaphus buselaphus*. However, in side view the horn cores have more forward curvature proximally and less backward curvature distally than living hartebeests, and *probubalis* might as easily be a subspecies of *Rabaticeras arambourgi* as of *Alcelaphus buselaphus*. Further examination of the fossils in question is desirable. Aboukir is thought to be of Amirian (= Middle Pleistocene) age. References to *Alcelaphus* at earlier sites, for example Arambourg's (1962 : 106) report for Ternifine, are probably based only on teeth and may be discounted. An alcelaphine, which was most probably *Alcelaphus buselaphus*, occurred in the recent past in Palestine, Jordan and more doubtfully Lebanon (Garrod & Bate 1937 : 215, fig. 7g and h; Ducos 1968 : 49, pl. 10; Clutton-Brock 1970 : 26; Hooijer 1961 : 45, pl. 2, fig. 2).

Alcelaphus lichtensteini or an immediately ancestral species is represented at Broken Hill,



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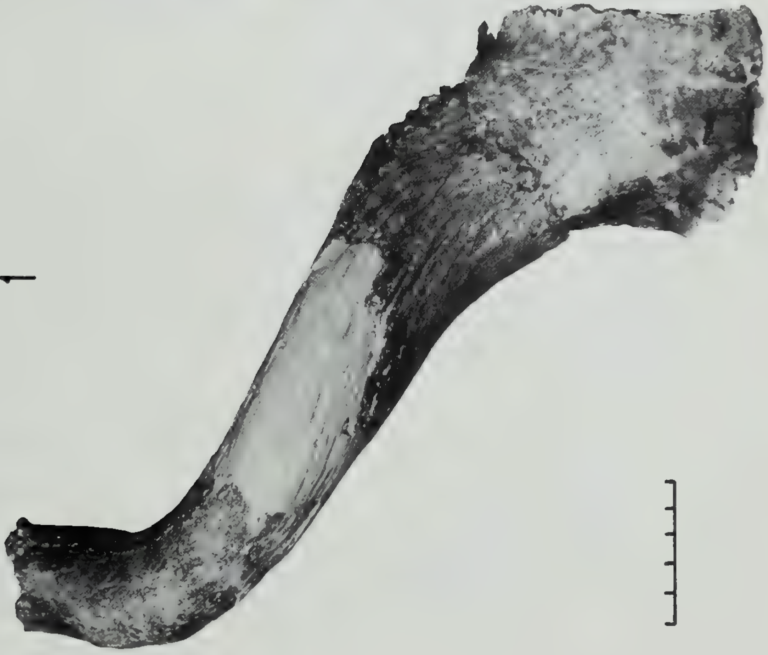

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Plate 33 (Scale = 50 mm)

Fig. 1 ***Beatragus antiquus*** holotype. Anterior view of right horn core from Bed I, BM(NH) M 21445.

Fig. 2 Medial view of same.

Zambia, among material previously assigned to *Connochaetes* (Leakey *in* Clark 1959 : 230). There is a base of a left and most of a right horn core BM(NH) M 12144, a left horn core M 12910 and two tips M 29486 and M 29487. The middle part of the right horn core curves sharply upwards, increases its thickness as it rises and shows transverse ridges towards the back of the dorsal side. Compared with *A. lichtensteini* it is very large and the top of the middle part is less twisted backwards towards the tip. This last character takes it closer to the supposed *Rabaticeras* ancestor, but one should not place too much weight on so slight a character.

The Pinjor Formation alcelaphine *Damalops palaeindicus* has already been compared with *Damaliscus agelaius* and was held to be related to the *Alcelaphus–Damaliscus* group. It differs from *Rabaticeras arambourgi* by the backward curvature of its horn cores in side view, the greater slope of the dorsal parts of the orbital rim, and probably by its less strongly sloping braincase roof. The horn core insertions also appear to lie further behind the orbits, which is probably linked with their being less upright. The absence of a parietal boss could imply that it is closer to *Rabaticeras* and *Alcelaphus* than to *Damaliscus*, and in this case the *Alcelaphus* lineage would become the only alcelaphine stock known to have existed outside Africa. For the moment this conclusion would be premature.

It is interesting that *Damalops palaeindicus* appears to have a close resemblance to the Laetolil partial cranium 1959.233, mentioned earlier on p. 390. The details are not relevant to the present paper, but the resemblance leads to the problem that if *Damalops* is related to the *Alcelaphus–Damaliscus* stock, how can it be that *Damaliscus niro* has more resemblance to the Laetolil cranium 1959.277 than to 1959.233? Interbreeding is possible between species of *Damaliscus* and *Alcelaphus* today, and one would not welcome their ancestry having been separate as long ago as in the Laetolil fauna. Alternative solutions are possible of course, but they need not be discussed until more fossils become available. Meanwhile a tentative phylogeny is shown in Fig. 28 (p. 400).

Genus ***BEATRAGUS*** Heller 1912

Type species. *Beatragus hunteri* (P. L. Sclater 1889).

Generic diagnosis. Medium-sized alcelaphines with horn cores inserted fairly uprightly over the back of the orbits, diverging strongly near the base but with long straight distal parts which are nearly parallel to one another, and with their long axis of cross-section set at a wide angle to the midline of the skull and not almost parallel to it as in most antelopes; strong transverse ridges. Where torsion is detectable in the horn cores it is anticlockwise on the right side. Supraorbital pits wide apart; preorbital fossae smaller than in *Alcelaphus* or *Damaliscus* but in the living species not as small as in *Parmularius*; P_2 usually absent.

Beatragus antiquus L. S. B. Leakey 1965

1937 *Beatragus hunteri* Schwarz : 55; pl. 2, fig. 9.
1965 *Beatragus antiquus* Leakey : 61; pl. 80.

Diagnosis. A species of *Beatragus* differing from living *B. hunteri* in its larger size; horn cores with more upright insertions in side view, diverging from the very base, sometimes less mediolaterally compressed in their lower parts, and with a less abrupt alteration in their course above the initial outward divergence; frontals wider and more convex in front of the horn core bases and less uparched between them.

Holotype. The lower part of a right horn core with much of the frontal anterior to the base, BM(NH) M 21445 found in 1935 (Pl. 33).

Horizon. The holotype is from Bed I, Olduvai Gorge. A few other specimens are known from Beds I and II. The species is also known from high in member G in the Shungura Formation, Omo.

Remarks. The paratype is an almost complete left horn core M 21446 found in Bed I in 1935 (Leakey 1965 : 61; pl. 80), and is probably from the same individual as the holotype. Other specimens in London are an incomplete right horn core M 21454 found in HEK II in 1935 and identified by Professor Wells in 1963, and parts of left horn cores M 14526 found in 1931 in Bed I, M 14539 found in 1932 in Bed I and M 29422 found in 1931 possibly in Bed I. The lower part of a right horn core M 26927 with part of the frontal and orbital rim from the surface of Bed I in 1931 is also probably of this species, perhaps a female. Specimens in Nairobi are a complete left horn core FLKN I 5123; the proximal half of a right horn core FLKN I 7132; part of a right horn core from MJTK I found in 1963; the proximal half of a left horn core 1962.067/4998 from FLKN II (base of Bed II); the lower half of a right horn core HWK East II 131 from level 1 which may be another female (Pl. 12, fig. 1); a frontlet S.217 with a nearly complete left horn core and most of the right found in 1971 at HWK East II in the rootlet clay of level 2 (Pl. 34); and a complete right horn core 1962.068/6654 from Kit K, a site at the first fault in upper Bed II.

The horn cores are less mediolaterally compressed than in *B. hunteri*, and both the holotype and paratype differ from the living species in having a larger posterior swelling at the very base of the horn core. The holotype horn core is inserted more uprightly in side view than in *B. hunteri*, diverges more from its base instead of curving gradually outwards, has localized up-arching of the frontals between the horn core bases and probably has a wider skull. All these features are also visible on the frontlet S.217. The horn core FLKN I 5123 is larger and thicker than in *B. hunteri*; it is less mediolaterally compressed, more divergent from its base in anterior view, and bent less backwards near the base and less upwards near the tip in side view. The horn core Kit K II 068/6654 is larger and longer than *B. hunteri* horn cores, and is still thicker than 5123. It is more mediolaterally compressed than 5123, perhaps as much as *B. hunteri*, but like 5123 the base passes directly outwards and in side view the bending is less pronounced than in *B. hunteri*. Its distal part passes inwards in anterior view more than in *B. hunteri* or other fossils. The more complete preservation than in 5123 shows that the insertion is probably more upright than in *B. hunteri* and that, as in *B. hunteri*, there is a shallow postcornual groove.

The partial right horn core from Olduvai which Schwarz (1937 : 55; pl. 2, fig. 9) identified as *B. hunteri* was almost certainly this species. The specimen was in Munich and was destroyed in the Second World War.

Beatragus is a long-lasting lineage. It differs from *Alcelaphus* in the more upright horn core insertions and their less posterior position on the skull, and from *A. buselaphus* in the lack of a united horn core pedicel. The abrupt alterations in horn core course and the coat colour of the living species are unlike *Damaliscus*, and the loss of P_2 distinguishes it from both *Alcelaphus* and *Damaliscus*. However, the small preorbital fossae and reduced premolar rows are approaches to *Parmularius*. In all the fossil *Beatragus* the long axis of the cross-section of the horn core bases is set at a wide angle to the midline of the skull. The same character can be seen in males of the living species, and we have taken it as another character whereby *Beatragus* can be distinguished from other genera.

MEASUREMENTS. Anteroposterior and mediolateral diameters at the base of horn cores of *B. antiquus* are:

Bed I BM(NH) M 21445	64·5 × 64·2	HWK East II 131	43·6 × 44·3
Bed I surface BM(NH) M 26927	50·9 × 41·5	Kit K II 068/6654	65·8 × 67·2

The lengths of FLKN I 5123 and Kit K II 068/6654 are 530·0 and 505·0 mm.

Measurements on the frontlet S.217 from HWK East II are:

Anteroposterior diameter of horn core at its base	52·3
Mediolateral diameter of horn core at its base	61·5
Minimum width across lateral surfaces of horn core pedicels	132·6
Width across lateral edges of supraorbital pits	73·5

COMPARISONS. A well-preserved and probably sub-adult cranium, FG 27-1, with most of the right and base of the left horn core was found just below Tuff H of the Shungura Formation, Omo, in 1967. It is the most complete specimen of *B. antiquus* so far discovered, and shows that the extinct species was larger than the living, and had relatively wider frontals and more of a parietal boss.

Like the living species it had a suite of generalized alcelaphine characters: a short braincase with quite a steeply inclined roof, a suture of the parietofrontals which is not very indented centrally, a median vertical ridge with flanking hollows on the occipital, an occipital surface facing mainly backwards, a basioccipital with moderate development of anterior tuberosities and longitudinal ridges, rather large foramina ovalia and the basisphenoid not strongly angled on the basioccipital.

A Kaiso horn core with the inscription 'KAISO C.94' is accompanied by a label reading *Beatragus* cf. *antiquus*. It is probably the horn core referred to as BM(NH) M 26623 by Cooke & Coryndon (1970 : 213). It is not impossible that it is alcelaphine, but having strong transverse ridges and no sinuses visible in the preserved part of the pedicel, it may be reduncine. We would not feel sure of an attribution to *Beatragus*.

The only South African fossils which seem to be *Beatragus* are a frontlet 16561 and other horn cores from Elandsfontein. The frontlet is from an antelope about the size of a wildebeest and has horn cores with slight mediolateral compression, some flattening of the lateral surface, a trace of a

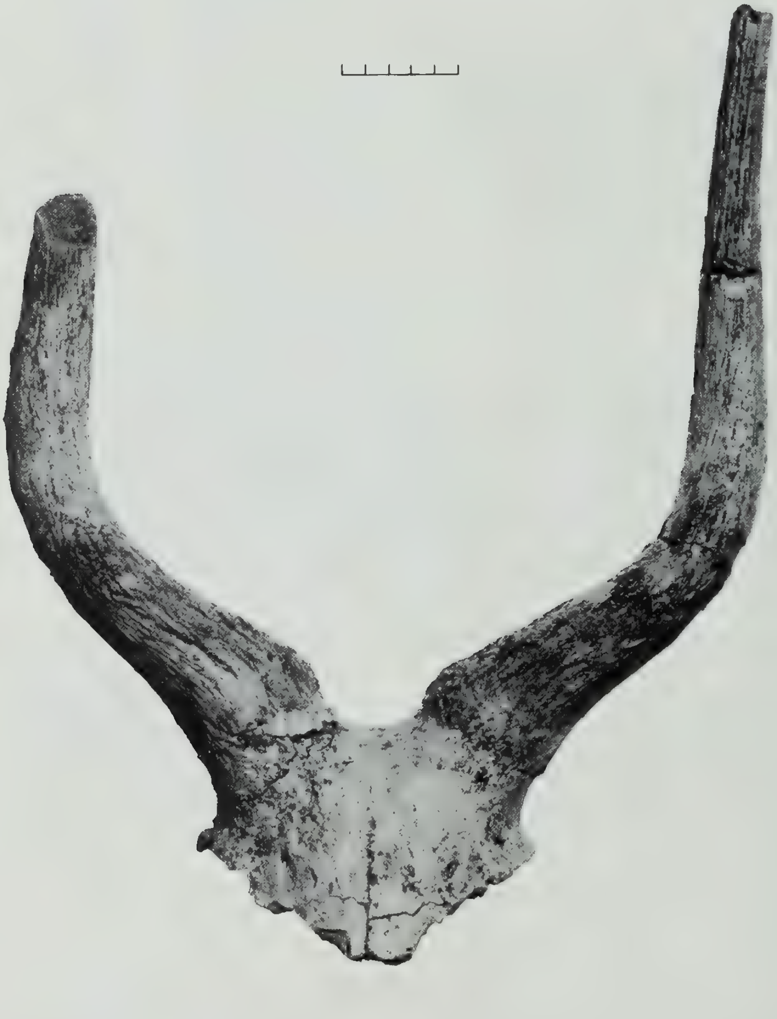


Plate 34 (Scale marked in centimetres)

Beatragus antiquus. Anterior view of frontlet S.217 from HWK East II.

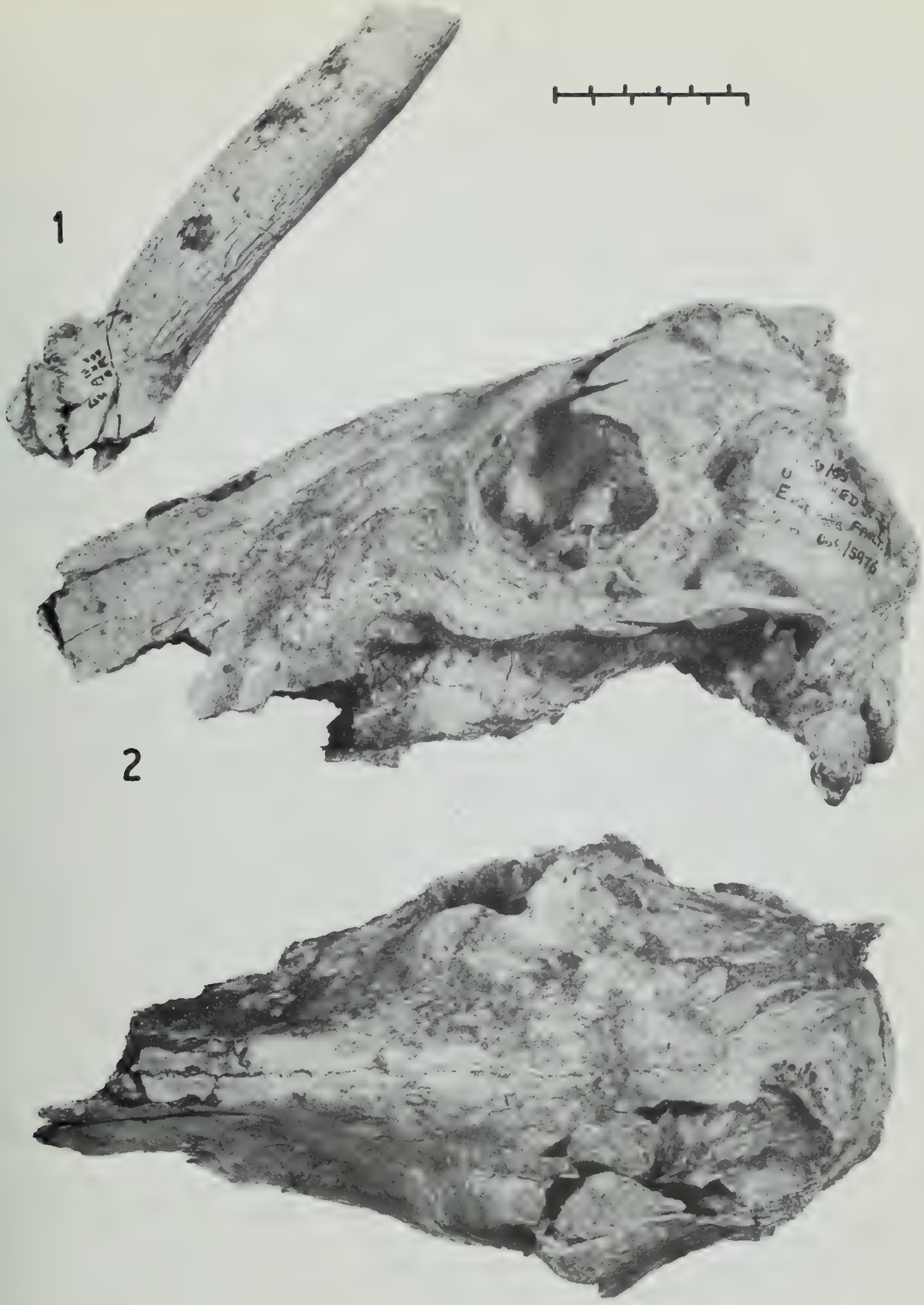


Plate 35 (Upper scale = 50 mm for horn core, lower scale = 50 mm for skull)

Fig. 1 ***Aepyceros melampus.*** Anterior view of left horn core, BK II 1957.662.

Fig. 2 **Alcelaphini** sp. 1. Lateral and dorsal views of partial skull, 1963.068/5976 from upper Bed IV.

posterolateral keel, transverse ridges, insertions above the back of the orbits, strong divergence from the very base and backward curvature in their lower parts. All this agrees with *B. antiquus*, but the horn cores differ in being short, inserted more obliquely in side view, not having a posterior basal swelling, and showing a much stronger inturning of their tips. This Elandsfontein form has some similarities to the central African populations of *Damaliscus lunatus lunatus*, but has larger and more massive horn cores. We believe that a relationship to *B. antiquus* is more likely.

Genus ***AEPYCEROS*** Sundevall 1847

TYPE SPECIES. *Aepyceros melampus* (Lichtenstein 1812).

Aepyceros melampus (Lichtenstein 1812)

1965 *Aepyceros* sp. indet. Leakey : 65.

REMARKS. There are a few horn cores of the impala at Olduvai. We have recorded the base of a left horn core THC I 1959.129, an incomplete left horn core with the midfrontal suture BK II 1957.662 (Pl. 35, fig. 1; Leakey 1965 : 65; Gentry 1966 : 104), and the basal part of a left horn core with the midfrontal suture and supraorbital pit BM(NH) M 26926 from the surface of SHK II in 1935. Two pieces of horn core from the surface of Bed II (register) or Bed IV (written on the horn cores), BM(NH) M 14551, are possibly *Aepyceros*.

MEASUREMENTS. Anteroposterior and mediolateral diameters at the base of horn cores of *A. melampus* are:

SHK II surface BM(NH) M 26926	35·7 × 29·3	BK II 1957.662	36·8 × 31·3

COMPARISONS. The occasional occurrence of impala horn cores at Olduvai contrasts with their abundance in the Shungura Formation at Omo. The impala at Omo is sufficiently different from the living one to be taken as a separate, ancestral species, at least until the base of member H. The Olduvai horn cores differ from many of the Omo specimens in being larger, diverging more strongly from the base upwards, and in lacking a posterior keel, and are therefore more like a majority of the living species.

Aepyceros melampus is represented at Peninj by parts of left horn cores A67.232 (WN64.318.CFG.MMG.BSC), A67.246 (WN64.97.MMG.BSC) and A67.255 (WN64.222. TMG(S).USC/MZ), a right mandible with one molar and part of another A67.409 (WN64.312), and possibly other pieces. In the later assemblage of the Kaiso Formation, *Aepyceros* is represented by part of a right horn core M 12592 (Cooke & Coryndon 1970 : 213), a left horn core M 12585, a left upper molar M 12596 and a left M_3 (the last being probably the *Gazella* cf. *wellsi* of Cooke & Coryndon 1970 : 213), all from Kaiso Village. The same authors also record a further horn core from the Nyawiega Early Kaiso assemblage now in the Uganda Museum. Two incomplete Laetolil horn cores in Berlin (Dietrich 1950 : 30, no figure) are labelled '*Aepyceros*' but have no catalogue numbers. The left horn core from Garussi korongo is of a large *Aepyceros*, but the right horn core from Ganeljuio (= Gadjingero by reference to the label for a gazelle maxilla) is less certainly *Aepyceros* and may be conspecific with the horn core of 'Aepycerotinae gen. et sp. indet.' (Dietrich 1950 : pl. 4, fig. 45) discussed on p. 351.

Aepyceros may be present at Makapansgat Limeworks. The morphology of a right mandible BPI M.759 is not sufficiently diagnostic for it to be definitely *Aepyceros* (cf. Wells & Cooke 1956 : 37) and it could be a large specimen of *Gazella vanhoepeni*. The portion of '*Aepyceros* cf. *melampus*' horn core M.654 (Wells & Cooke 1956 : 36, fig. 19) has strong V-shaped transverse ridges on one side and an approach to a keel on the opposite side as in *Aepyceros*, but is very large. However, a large unnumbered right mandible with P_2–M_2 has a small P_4 with the paraconid–metaconid fusion of *Aepyceros* as well as a small P_2, so perhaps a very large *Aepyceros* was indeed present. Some isolated upper molars (right M.43, M.52 and M.763; left M.45, M.49 and M.51) are larger than *G. vanhoepeni* and have strong mesostyles and the posterior lobe less transversely elongated than the anterior one; they also could be of *Aepyceros*.

Indeterminate Alcelaphini

Some alcelaphine fossils at Olduvai are difficult to fit into the general picture.

SPECIES 1. A partial skull 1963.068/5976 from east of the second fault in upper Bed IV or the Masek Beds is well preserved and not crushed but lacks teeth and both horn cores (Pl. 35, fig. 2). The braincase is short and strongly angled on the face and the horn core insertions very oblique in side view, all of which would fit *Parmularius*. However, there is definitely no trace of a parietal boss, and the shallow preorbital fossa occupies a larger area than would be admissible for *Parmularius*. The best suggestion, but not an entirely convincing one, is that this is a member of the *Rabaticeras–Alcelaphus* lineage later than the Bed III fossils and in which there has taken place a decline in size, steepening of the braincase roof, and lowering of the inclination of the horn core insertions.

Measurements on this cranium are:

Skull width across posterior side of orbits	123·0
Width across lateral edges of supraorbital pits	58·6
Length from back of frontals to top of occiput	45·9
Maximum braincase width	77·3
Skull width across mastoids immediately behind external auditory meati	97·6
Occipital height from top of foramen magnum to top of occipital crest	39·4
Width of anterior tuberosities of basioccipital	22·3
Width of posterior tuberosities of basioccipital	27·7

SPECIES 2. A cranium with the basal halves of both horn cores S.208 was collected in 1970 from the Lemuta Tuff Member (Pl. 31, fig. 3; Pl. 32, fig. 1). It has some resemblance to *Rabaticeras arambourgi*, and agrees in size with the JK2 III material of this species. However, it differs in having its horn cores inserted less uprightly in side view and more widely apart in anterior view, and in the frontals between the horn core bases being less raised. Its braincase is low and wide, in contrast to the Elandsfontein cranium of *R. arambourgi*. A partial palate with very worn left M^2 and M^3 was also collected with the cranium; it appears to have root sockets for only two premolars. It is difficult to assess this fossil. One possibility is that it is directly ancestral to *Alcelaphus lichtensteini* rather than to the Bed III *R. arambourgi*. The great width across the braincase and across the horn core insertions are the only basis for this suggestion, while the probable absence of P^2 is a difficulty. The consequent diphylety of *Alcelaphus* would necessitate changes of nomenclature. It is awkward to relate the fossil to *R. arambourgi* if the latter is ancestral to *Alcelaphus buselaphus*, since horn core insertions would first have to become more upright in Bed III times, then more inclined for a second time in the living hartebeest.

Measurements on the cranium S.208 are:

Anteroposterior diameter of horn core at its base	54·7
Lateromedial diameter of horn core at its base	42·2
Minimum width across lateral surfaces of horn core pedicels	128·0
Maximum braincase width	94·4
Occipital height from top of foramen magnum to top of occipital crest	47·5
Width of anterior tuberosities of basioccipital	25·9
Width of posterior tuberosities of basioccipital	33·2

SPECIES 3. Leakey (1965 : 68(c)) referred four horn cores to a category 'cf. Caprini'. These were a left horn core with part of the frontals, orbit and parietal SHK II 1953.280, parts of two other horn cores SHK II surface 1957.92 and SHK II 1953.234, and a right horn core F.3000 with part of the orbit and a good deal of the parietal from the surface of Bed II in 1941 (Pl. 40, figs 1–2). An incomplete frontlet with horn core bases, 1953.067/5460 from BK II East, is likely to be a smaller individual of the same species. The two most complete specimens have horn cores without transverse ridges, inserted rather uprightly and close together on short pedicels above the orbits, hollowed frontals and no parietal boss. All these characters are resemblances to *Rabaticeras arambourgi*, but these horn cores have more mediolateral compression and are nearly straight with only a very slight forward curvature, divergence or torsion. The braincases are as steeply

inclined as in the Bed III and Elandsfontein *Rabaticeras*, and certainly more inclined than in the *Rabaticeras*-like specimen from the Lemuta tuff. Two alternatives seem to be possible for their classification. One, which we favour, is to regard them as a variant within the *R. arambourgi* lineage, and another is to regard them as possibly linked with the 'Villafranchian' *Numidocapra crassicornis* Arambourg (1949 : 290) from Ain Hanech, Algeria. The holotype of this is very large with long horn cores inserted close together on short pedicels above the orbits. The horn cores curve forwards as they rise, nearly parallel to one another, and are probably without transverse ridges or keels. The braincase is strongly bent downwards and has no parietal boss. If the Olduvai horn cores are related to *Numidocapra*, it would be good to know whether they should be classified as Caprinae similar to *Procamptoceras brivatense* Schaub (1923 : 282, figs 1–2) from the Villafranchian of Senèze, France, or as Alcelaphini.

Anteroposterior and mediolateral diameters at the base of the two measurable Olduvai horn cores are:

SHK II 1953.280 52·9 × 39·4 Bed II surface 1941 F.3000 64·6 × 44·1

A frontlet with both horn cores 794 and an almost complete right horn core 839 from Elandsfontein resemble the horn cores SHK II 1953.280 and F.3000 in some characters. They agree in overall size, and in that the horn cores are of normal length, mediolaterally compressed, almost parallel in anterior view, have a clockwise torsion in the right horn core, are without keels or transverse ridges, and with only a very slight or absent postcornual fossa. The midfrontal and parietofrontal sutures are simple and the parietofrontal suture lacks a dorsal indentation centrally. Paired swellings occur in front of the horn cores. The Elandsfontein remains differ from the Olduvai fossils in the more pronounced torsion of the horn cores, their more oblique plane in side view, the lack of any forward curvature, the insertions being possibly wider apart in anterior view and the braincase less steeply angled on the facial axis. It seems unlikely that they have any connection with the Olduvai fossils.

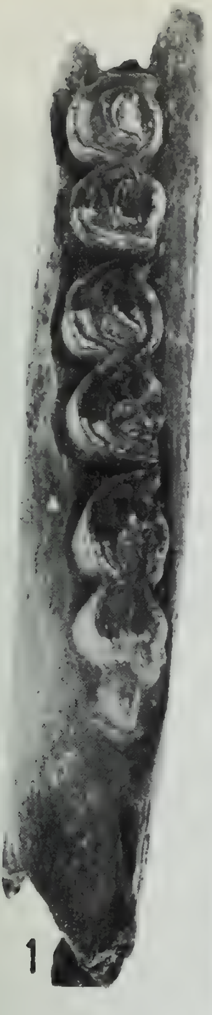
SPECIES 4. A horn core FLKN I 7884 from level 6, a horn core with a crushed braincase FLKN I 5196 P.P.R.10 from level 5 and part of a horn core from Bed I BM(NH) M 14521 could represent a small alcelaphine species (Pl. 40, figs 4–5). The horn cores are very laterally compressed, without keels or transverse ridges, notably long in comparison with their slenderness, and strongly spiralled. However, the first specimen is without its base, and the second is no longer attached to its braincase, so there is no certainty about the planes of insertion or direction of the horn cores' course. A possible fit of the horn core 5196 to its braincase suggests that the horn cores may be inserted obliquely in side view, curving upwards and less backwards from the base. If 5196 were a right horn core its anticlockwise torsion would be the reverse of the situation found in the larger *Rabaticeras*. The hollowed horn core pedicel of 5196, its basioccipital with small localized anterior tuberosities almost as wide apart as the posterior ones, and the very slight development of longitudinal ridges behind the anterior tuberosities could be equally as consistent with membership of the tribe Antilopini or even of the Neotragini as with the Alcelaphini.

Measurements on FLKN I 5196 P.P.R.10 are:

Anteroposterior diameter of horn core at its base	26·8
Mediolateral diameter of horn core at its base	18·7
Width of anterior tuberosities of basioccipital	18·6
Width of posterior tuberosities of basioccipital	22·9

Four small probably alcelaphine mandibles from Olduvai could conceivably belong to the same species as the horn cores, although there is no association between them. They are right FLKN I 1293 from levels 1–2 and left FLKN I 137 from levels 1–3, left F.109 from the surface of Bed I in 1941, and left F.102 from the surface of Bed II in 1941. They have horizontal rami markedly deeper below the molars than below the premolars, paraconid almost fused with the metaconid on P_4, a small P_2, and molars of alcelaphine appearance. Two alcelaphine left mandibles HWK EE 1156 and the more fragmentary 4302 from middle Bed II are also small and deep-jawed, but not so pronouncedly deep under the molars. The paraconid and metaconid are not fused on P_4, and the P_2 had been lost in life.

Measurements on these mandibles are:



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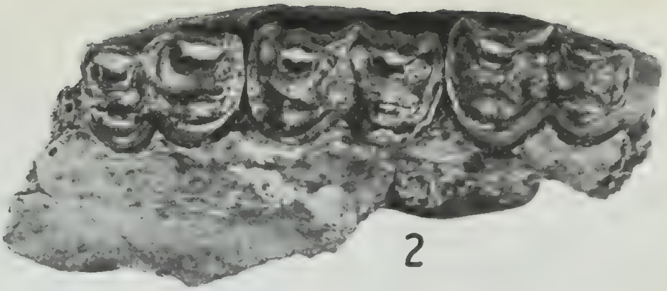

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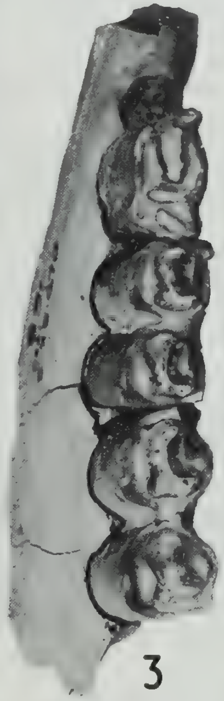

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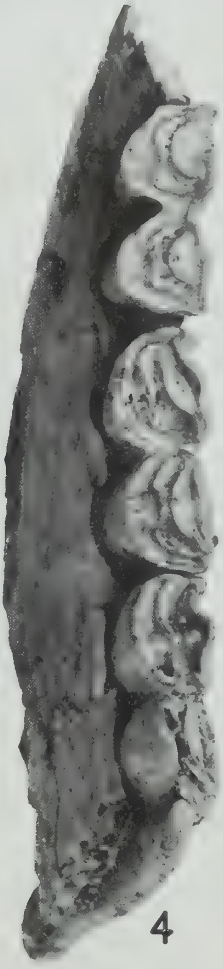

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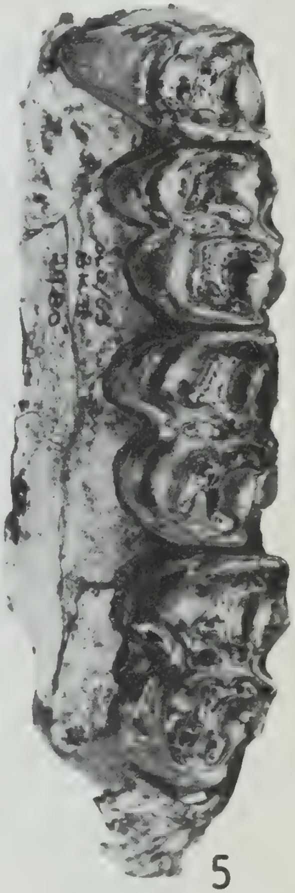

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Plate 36 (Scale = 25 mm)

Large alcelaphine dentitions, size group (i).

Fig. 1 Left M_1–M_3, JK2 III A.3261.

Fig. 2 Left M^1–M^3, BK II 1963.670.

Fig. 3 Left P_4–M_2 with root of P_3, BK II 1952.148.

Fig. 4 Left M_1–M_3, MNK II 2070.

Fig. 5 Left P^4–M^3, BK II 1963.2980.

	F.109	F.102	HWK EE 1156
Occlusal length M_1–M_3	50·5	–	46·0
Occlusal length M_2	16·5	–	15·7
Occlusal length M_1	14·4	15·3	13·0
Occlusal length P_2–P_4	–	23·5	11·7 (P_3–P_4)

Limb bones apparently belonging to antilopine-sized alcelaphines are known from DK I, FLKN I, HWK East lower II and HWK EE middle Bed II. They are of a size to be conspecific with the above horn cores and/or mandibles, but there is no direct association. Rather small alcelaphine limb bones continue to occur in later sites, but another possible attribution for these would be to *Damaliscus agelaius*.

The mandibles have some resemblance to the Omo '*Antidorcas* sp.' of Arambourg (1947 : 390; pl. 30, fig. 3) which is not larger than the Olduvai pieces (cf. Gentry 1966 : 67). The Omo mandible agrees best with HWK EE 1156 in its less marked posterior depth, its very short premolar row, and lack of P_2. Further teeth from the Shungura Formation, perhaps of the same unknown species, have been recovered by the American group, e.g. L.465-22 from member F and L.526-4 and L.614-1 from member G.

Measurements of alcelaphine dentitions and limb bones

We cannot identify alcelaphine dentitions from Bed II and Bed III to generic and specific level. All that is possible is to assign the more complete ones to two size classes (Fig. 30; Pls 36, 37). The teeth have a lower level of occlusal complexity than is usual in living alcelaphines. A parallel size system has been set up for limb bones.

SIZE GROUP (i). According to measurements of the teeth on the neotype skull BM(NH) M 21447 of *Megalotragus kattwinkeli* the largest dentitions belong to this species. The teeth have a simple occlusal pattern. Measurements on two maxillae of this size group are:

	BK II 1963.2980	BK II 1963.458 (immature)
Occlusal length M^1–M^3	89·1	–
Occlusal length M^2	31·0	36·2

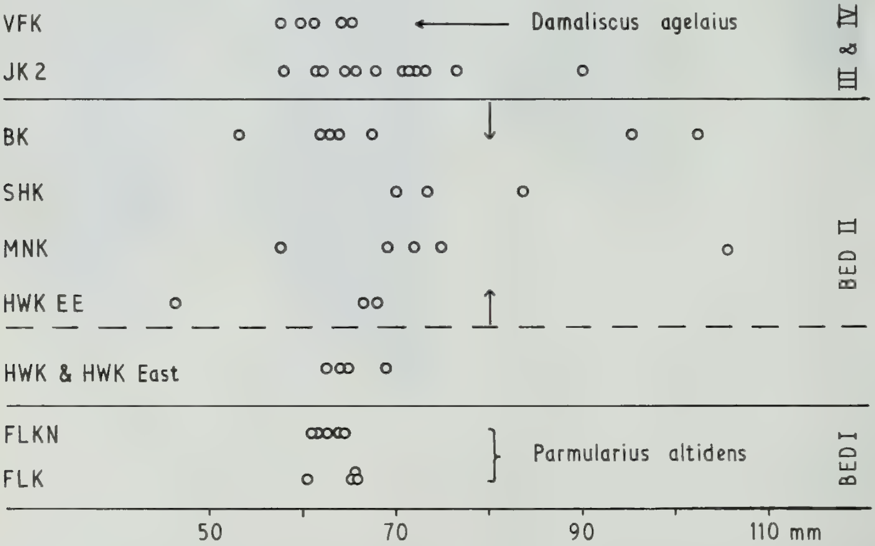


Fig. 30 Length of M_1–M_3 in Olduvai Alcelaphini to show the size classes (i) and (ii) in Bed II. The vertical arrows at 80 mm divide size class (i) from (ii). Earlier and later fossils are shown for comparison. The dashed line demarcates lower Bed II.

Measurements on the more complete mandibles of this size group are:

	MNK II	SHK II	SHK II or BK II	BK II
	2070	1957.256	068/5536	1952.622
Occlusal length M_1–M_3	105·7	*c.* 84·0	90·8	–
Occlusal length M_2	35·2	26·0	–	–
Occlusal length P_3–P_4	–	–	–	31·3

	BK II	BK II	JK2 III	JK2 III
	1957.713	1957.979	A.2828	A.3261
Occlusal length M_1–M_3	102·2	95·3	–	89·9
Occlusal length M_2	30·6	31·1	27·4	29·1
Occlusal length P_3–P_4	–	*c.* 26·0	–	–

Measurements on the M_2s of nine mandibles from BK II, including two from the mandibles whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_2	9 (left+right)	28·9	22·2–33·5	3·4	1·15
	5 (left only)	27·3	22·2–31·1	3·7	1·65

A very few dentitions are slightly smaller, but still large, and are probably *Connochaetes taurinus olduvaiensis*. The only measurable one is a maxilla, BK II 1963.670:

Occlusal length M^1–M^3	66·7	Occlusal length M^2	27·5

The largest limb bones belong with these teeth and are presumably *Megalotragus kattwinkeli* and possibly some *Connochaetes taurinus olduvaiensis*. Measurements of length and least thickness are:

Tibiae	BK II Ext 1953.417	360 × 35·8	BK II 1957.1379	325 × 34·9
	BK II 1963.2680	374 × 38·0	BK II 1963.3036	330 × 30·8
Metatarsals	MNK II 169	300 × 26·8	MNK II 2718	273 × 20·7
	SHK II 1957.231	288 × 24·2	SHK II 1957.839	271 × 24·1
	SHK II 1967.731 (immature)	261 × –	BK II 1953.067/5508	290 × 26·1
	BK II Ext 1953.416	311 × 28·6		
Radii	SHK II 1957.283	337 × 35·4	BK II Ext 1953.426+428	317 × 34·6
	BK II 1963.854+863	307 × 40·1		
Metacarpals	MNK II 2704	257 × 30·7	SHK II 1957.558	237 × 27·4
	SHK II 1957.1350	247 × 28·6	BK II 1952.219	242 × 33·3
	BK II 1963.2609	264 × 26·9	JK2 III A.1272	263 × 22·1

Two metatarsals in this size group are shorter than those listed above and have low and wide distal condyles. They are probably *Connochaetes taurinus olduvaiensis*. Measurements of their length and least thickness are:

MNK II 752	239 × 25·0	BK II 1953.067/5509	249 × 29·2

SIZE GROUP (ii). Dentitions and limb bones smaller than those of the above group are probably of *Parmularius angusticornis* and *Damaliscus niro* but may include some *Connochaetes*. The teeth are about the size of living *Alcelaphus buselaphus* and slightly larger than Bed I *Parmularius altidens*. Measurements on mandibles in this size group are:

	MNK II	MNK II	MNK II	SHK II	SHK II
	136	976	2403	1957.268	1957.455
Occlusal length M_1–M_3	69·3	72·4	75·0	70·3	73·5
Occlusal length M_2	23·5	22·5	23·0	22·6	24·5
Occlusal length P_2–P_4	21·5	–	–	–	–

	BK II 1963.24	BK II 1963.941	BK II 1963.1065	BK II 1963.1442
Occlusal length M_1–M_3	63·9	67·6	–	c. 62·0
Occlusal length M_2	20·2	23·1	21·4	20·5
Occlusal length P_2–P_4	–	–	c. 23·0	–

	BK II Ext 1953.76	JK2 III A.1444	JK2 III A.2060	JK2 III A.2091
Occlusal length M_1–M_3	63·0	76·7	75·8	–
Occlusal length M_2	22·0	24·2	23·8	20·5
Occlusal length P_3–P_4 (P_2 missing)	–	–	–	22·7

	JK2 III A.2780	JK2 III A.2934	JK2 III A.3012
Occlusal length M_1–M_3	72·3	64·5	72·9
Occlusal length M_2	22·7	19·5	24·2
Occlusal length P_2–P_4	–	c. 31·4	–

	JK2 III B.FQ4-10	JK2 III B.FQB-1	JK2 III B.FL2-21	JK2 GP8 III GN 16
Occlusal length M_1–M_3	71·0	71·2	–	65·3
Occlusal length M_2	22·9	23·6	25·8	20·2
Occlusal length P_2–P_4	11·2	–	–	–

Immature mandibles BK II 1963.291, BK II 1963.2550 and JK2 III A.2157 have deciduous P_2–P_4 measuring 38·0, 37·1 and 40·3. BK II 1963.067/1635 has deciduous P_3–P_4 (deciduous P_2 was missing in life) measuring 27·6 mm.

Measurements on the M_2s of 10 mandibles from BK II, including five from the mandibles whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_2	10 (left+right)	20·4	16·5–23·1	1·7	0·55
	6 (left only)	20·2	16·5–23·1	2·3	0·93

Measurements of length and least thickness of the limb bones in this size group are:

Tibiae	MNK II 167	333 × 29·5	JK2 GP8 III GN 22	310 × 22·3
Metatarsals	SHK II 1957.933	234 × 17·9	JK2 III A.1671	271 × 17·2
Radii	SHK II 1957.209	262 × 30·1	BK II 1957.26	244 × 27·0
	JK2 III A.1305+1491	264 × 26·1		
Metacarpals	SHK II 1957.208 (immature)	218 × 17·1	SHK II 1957.330	220 × 18·8
	BK II 1957.1381	227 × 20·3	BK II 1963.3229	224 × 18·4
	JK2 III A.1592	224 × 18·8		

Associated femur BK II Ext 1953.067/5364 259 × 25·9, tibia BK II Ext 1953.067/5363 319 × 25·9 and metatarsal BK II Ext 1953.067/5506 246 × 19·3.

Plate 37 (Scale = 25 mm)

Alcelaphine dentitions, size group (ii).

Fig. 1 Left P_4–M_3, SHK II 1957.268.

Fig. 2 Left M_1–M_3, BK II 1963.941.

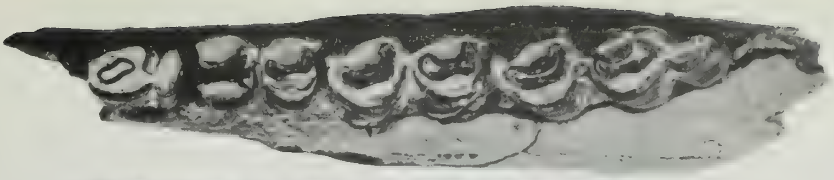
Fig. 3 Left P_3–M_3, JK2 III 068/6692.

Fig. 4 Right P_3–M_3 with socket for P_2, JK2 III A.2934.

Fig. 5 ***Parmularius altidens.*** Left P^3–M^3, FLKN I 1136. Same scale as above.

Fig. 6 **Alcelaphini** indet. Lateral view of left mandible, HWK East II 168. For this illustration the scale = 50 mm.

1



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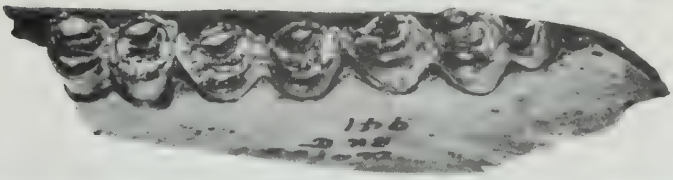

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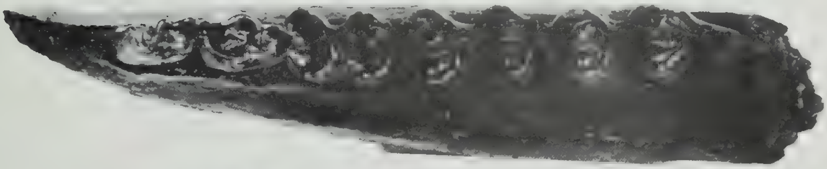

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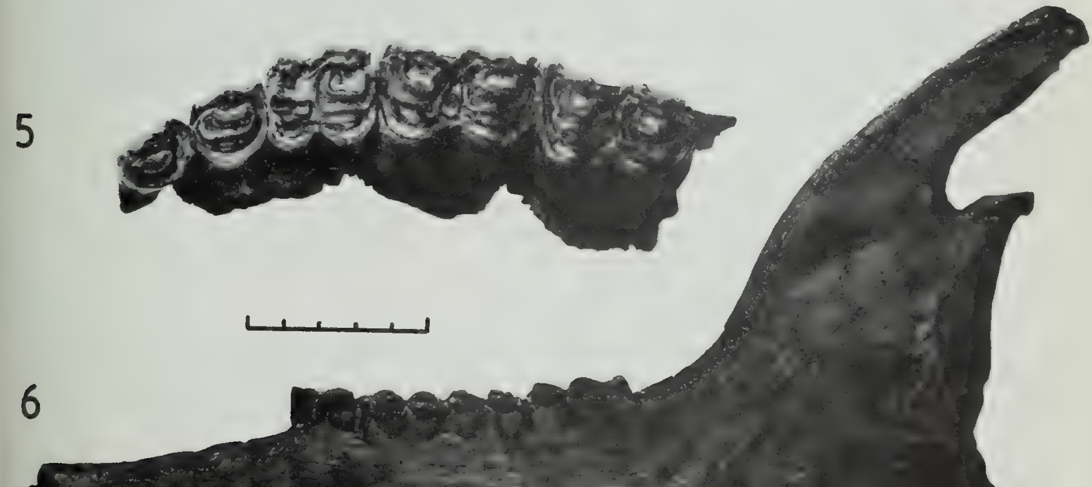


The smallest dentitions and limb bones of this size group are likely to belong to a smaller alcelaphine than *Parmularius angusticornis* or *Damaliscus niro*, possibly *D. agelaius*. We cannot separate clearly a third size group, but included here would be a maxilla, MNK Skull Site 89:

Occlusal length M^1–M^3 52·9 Occlusal length M^2 18·9

Measurements on the smallest of the mandibles in this size group are:

	MNK II 1725	BK II 1957.21	BK II 1957.1452	JK2 III B.FFM3-14
Occlusal length M_1–M_3	*c.* 57·7	–	53·2	–
Occlusal length M_2	17·4	19·5	16·5	19·0
Occlusal length P_2–P_4	–	–	18·7	–

	JK2 III A.384	JK2 III A.1372	JK2 III 068/6692	JK2 GP8 III Sec 6
Occlusal length M_1–M_3	–	58·0	62·0	61·9
Occlusal length M_2	–	19·3	20·5	20·1
Occlusal length P_3–P_4	20·4	–	23·9	–

Measurements on the smallest of the limb bones in this size group are:

Tibia	BK II 1957.1261	243 × 18·0		
Metacarpals	BK II Ext 1953.337	202 × 18·0	BK II 1963.2311	191 × 17·8
	JK2 GP8 III GN	193 × 17·8		

Tribe **NEOTRAGINI**

At the present day this tribe consists of 14 species of small antelopes. Their horn cores are sometimes short and always of small cross-sectional area, not very compressed, inserted widely apart and above the back of the orbits, straight or curved slightly forwards but not backwards, not very divergent and occur nearly always only in males. The midfrontal and parietofrontal sutures are not very complicated, the braincase is little angled on the facial axis but its back part is often downturned, supraorbital pits are small and a preorbital fossa is present. There are generally no basal pillars on the molars, there are no outwardly bowed ribs between the styles on the lateral walls of the upper molars, the enamel outer walls of the molars tend to be straight and with pointed rather than rounded corners.

The genera in the tribe are:

Neotragus H. Smith 1827 (including *Nesotragus*), with three living species,
Madoqua Ogilby 1837 (including *Rhynchotragus*), with five living species,
Oreotragus A. Smith 1834, with one living species,
Dorcatragus Noack 1894, with one living species,
Raphicerus H. Smith 1827, with three living species,
Ourebia Laurillard 1841, with one living species.

Ourebia has a number of reduncine-like characters and is possibly not of this tribe. *Pelea* may have to be included in the Neotragini, unless the single species, *P. capreolus* the Vaal rhebok, should turn out to belong in the Antilopini (Oboussier 1970) or in the Caprinae. So few neotragine fossils have been found that a fuller discussion of the tribe is unnecessary.

A pair of Olduvai horn cores with a small part of the frontal FLKN I 10229 are small enough to belong to a neotragine species (Pl. 40, fig. 3). They are too incomplete for definite orientation, but what appear to be the front edges may be less concave in side view than in living neotragines. *Raphicerus* would have been a reasonable attribution, except that sinuses are present in the frontals. These throw doubt on the horn cores being neotragine at all.

An incomplete right mandible FC West II 167 with deciduous P_2–P_4 is extremely small and probably neotragine.

The Olduvai scapula called *Nesotragus moschatus* subsp. by Schwarz (1937 : 40) was destroyed in Munich during the Second World War.

OTHER FOSSIL NEOTRAGINES. A number of Laetolil horn cores in Nairobi (left 1959.107 and 1959.570, right 1959.222, 1959.472 and 1959.571) can be referred to *Madoqua* by their oblique insertions, medial keels and slightly less marked lateral keels. 1959.570 is rather larger than the others. They agree with the Berlin horn cores of *Praemadoqua avifluminis* Dietrich (1950 : 34; pl. 1, figs 3–4). We saw twelve such horn cores in Berlin.

Several Laetolil dentitions and isolated teeth are also referable to *Madoqua* on their overall size. In Nairobi there are left maxilla 280, right maxilla 163 + 164, two right upper molars numbered 165, left mandibles 58, 70, 115, 156, 157, 159, 160 + 161, 297, 300 + 301, 307, 449, 604, 607 + 612 and 613, right mandibles 154, 155, 278, 295, 305, 448, 450, 451, 606, 608, 610 + 611, and immature right mandibles 158 and 306 which were all found in 1959. In London there are left mandibular pieces BM(NH) M 15107 and M 15108, right mandibles M 15109, M 15111, M 26782, M 26783 and immature left mandible M 26781. The premolar row length, as deduced from 154, 278, 297, 307, 607 + 612 and 610 + 611, has a similar proportion to the molar row length as in extant *Madoqua*. The very small back lobe of the M_3s, in all except M 15109, agrees with the subgenus *Rhynchotragus* within *Madoqua* and not with the subgenus *Madoqua* s. s. in which the lobe has completely gone. The lobe is absent in M 15109. These dentitions agree with those assigned to *Praemadoqua avifluminis* by Dietrich (1950 : 34; pl. 3, figs 25–26, the M_3 of fig. 25 being an odd tooth which has been stuck to the rest).

A complete right metatarsal 1959.218, from Laetolil and now in Nairobi, has a length of 94·5 and least thickness of 7·3. It is slightly shorter and relatively thicker than living *Madoqua* (Fig. 31), but otherwise is about the right size and with appropriate morphology. It differs from the suni *Neotragus moschatus* in its greater size and length and in the more upright outer anterior edges of the distal condyles, the larger ectocuneiform facet at the proximal end, the less marked flange medially at the top of the posterior side, and the absence of two foramina at the top of the posterior side. It is too large for the other (i.e. not east African) species of *Neotragus*, too small for *Raphicerus*, *Dorcatragus* and *Ourebia*, and not short enough for *Oreotragus*. The two duiker genera *Cephalophus* and *Sylvicapra* can be eliminated because there is no longitudinal groove on the anterior surface.

Two right mandibular pieces from Laetolil in Nairobi 1959.153 and 1959.447, the left mandible BM(NH) M 26778 and perhaps the left M_3 M 26779 are larger than the mandibles of contemporaneous *Madoqua* and about the size of *Raphicerus*. The P_4s on 1959.447 and M 26778 are unlike *Ourebia* and quite similar to *Raphicerus*. The molars of M 26778 retain basal pillars.

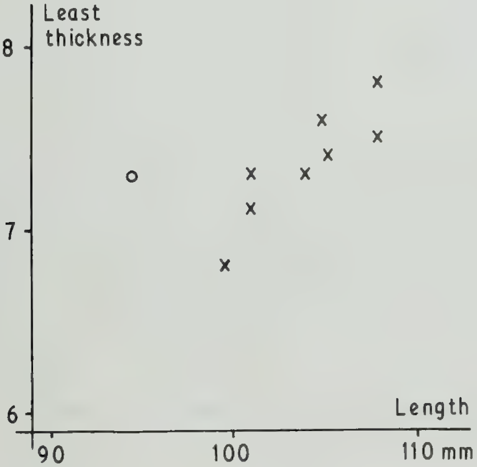


Fig. 31 Proportions of *Madoqua* metatarsals.

X = living east African *M. kirki*, O = Laetolil metatarsal 1959.218, assumed to be conspecific with the *Madoqua* fossil horn cores from that area.

The mandibles agree in size and morphology with those assigned by Dietrich (1950 : 25; pl. 2, fig. 13) to the smallest of his three gazelle species, *Gazella hennigi*, but they are too small for a gazelle.

A right upper molar, BM(NH) M 25708 from Kanjera, is probably of *Ourebia*.

A horn core, a mandible and the distal end of a metatarsal represent the Neotragini in members E, F and G of the Shungura Formation, Omo.

A couple of crania, some frontlets and horn cores and many dentitions from Elandsfontein are of *Raphicerus*. They represent a larger antelope than the living steinbok or grysbok, their supraorbital pits are not obscured by overgrowth of the frontals, the horn cores are set more obliquely in side view, and a few of the larger horn cores tend to have a posterolateral keel. The horn cores on one frontlet, 14153, have a mid-lateral keel as well and resemble some neotragine horn cores from Langebaanweg. The Langebaanweg material, consisting of a right horn core and associated right maxilla both numbered L.12238 and several other horn cores and dentitions, seems likely to be an early *Raphicerus*. The horn cores still have a more irregular cross-section than those at Elandsfontein and they show a posterolateral keel, a tendency to an anterolateral longitudinal concavity and other irregular keels or ridges. They are also larger as a whole. The Elandsfontein and Langebaanweg material make it clear that living *Raphicerus* has evolved from ancestors with larger and obliquely inserted horn cores. Further fossils of *Raphicerus* coming to light in east Africa will have to be compared with this South African material. The size diminution in the history of *Raphicerus* contrasts with the size stability of the Laetolil fossil *Madoqua*.

There are some other *Raphicerus* fossils in South Africa. Horn cores from Baard's quarry at Langebaanweg are smaller than at Elandsfontein, and cranial remains from the late sites of Melkbos (Hendey 1968 : 111) and Swartklip (Hendey & Hendey 1968 : 61) are indistinguishable from living *Raphicerus*. A right horn core BPI M.478 from Makapansgat Limeworks is like those at E quarry Langebaanweg, and was published as *Cephalophus pricei* (Wells & Cooke 1956 : 12, fig. 6). The tooth rows assigned by the same authors to *C. pricei*, one of which is the holotype, are from a bushbuck-sized tragelaphine.

A frontlet BPI M.476 of a supposed *Oreotragus* and some small dentitions from Makapansgat Limeworks were referred to *O. major* by Wells & Cooke (1956 : 35, figs 17–18). This name had been founded by Wells (1951 : 167, fig. 1) on a large *Oreotragus* skull with palate BPI M.651 from a red breccia deposit of unknown age in the Makapan valley. The Limeworks frontlet has very short horn cores with some degree of anteroposterior compression, and is not very like the *O. major* holotype. The Limeworks dentitions have premolar rows which were probably slightly longer relative to the molar rows than in the living klipspringer *O. oreotragus*. The frontlet M.476 differs from the Makapansgat *Raphicerus* horn core M.478 by its shortness, more upright insertion and a more regular shape of cross-section.

Tribe **ANTILOPINI**

Living members of the Antilopini are the springbok, gerenuk, dibatag, several species of gazelle and the Indian blackbuck which has spiralled horns. They are small to medium-sized, long-legged, grazing or browsing antelopes often adapted to life in arid areas. The skulls are not very distinctive at tribal level, especially when fossil forms are taken into account. The main skull features are: horn cores inserted above or partly behind the orbits, horns not always absent in females, face and braincase moderately long, braincase little angled on the facial axis, parietofrontals' suture complicated, preorbital fossae present, mastoids large, basioccipital moderately long and not narrowing anteriorly except in some early forms, premaxillae large and long, infraorbital foramen above P^2 or P^3, teeth of early forms brachyodont and with basal pillars but becoming hypsodont and losing basal pillars during evolution, central cavities with a simple outline, P_4s without fusion of paraconid and metaconid to form a complete medial wall anteriorly except in some east Asian gazelles.

Gazella Blainville 1816 is an exceptional genus among bovids in spanning both the Palaearctic and Ethiopian faunal realms. At present it occurs no further south in Africa than central Tanzania.

The species may be grouped as follows:

1. An east Asian group of two or three species frequently placed in the subgenus *Procapra*. Related to them is the Persian gazelle *Gazella subgutturosa*.

2. A second main Palaearctic group comprises the various gazelles of Arabia and the Near East, *G. bennetti* extending into India, and the widespread *G. dorcas* (Linnaeus 1758) of north Africa which includes *G. dorcas pelzelni* Kohl 1886, of the northern Somalia coastal plain. This whole group is likely to form one or two species.

2a. Possibly related to group 2 are *G. cuvieri* (Ogilby 1841) of the Atlas region, *G. leptoceros* (F. Cuvier 1842) of sandy areas of the Sahara and *G. spekei* Blyth 1863 of Somalia.

3. The west African *G. rufifrons* Gray 1846 and *G. thomsoni* Günther 1884 seem to be a truly Ethiopian group slightly larger than *G. dorcas* and with a different skull morphology. Despite the skull similarities between the two species, *G. rufifrons* has a longer premolar row than *G. thomsoni*.

4. A second Ethiopian group is constituted by the three large species *G. dama* (Pallas 1766) of west Africa, *G. soemmerringi* (Cretzschmar 1826) of Somalia and the Sudan, and *G. granti* Brooke 1872 of east Africa.

We might therefore expect to find at Olduvai relatives of groups 3 and 4, but we should regard it as a matter of note if gazelles closely related to group 2 were found. In fact the Olduvai gazelle is rather poorly known, but does seem to be related to group 3.

Antidorcas Sundevall 1847 is a genus of which the South African springbok *A. marsupialis* (Zimmermann 1780) is the only living species. Living springbok females are bigger-horned than gazelle females, and though the horns of springbok females are mostly less bent backwards than in the males, Lange (1970 : 73) found sexual dimorphism in the skulls of springbok to be less than in gazelles.

Litocranius walleri (Brooke 1878) and *Ammodorcas clarkei* (O. Thomas 1891), the African gerenuk and dibatag, do not occur at Olduvai. Leakey (*in* Clark 1959 : 230) identified some limb bones from Broken Hill, Zambia, as *Litocranius*, but some skull parts would be preferable for a definite identification (see p. 436).

Antilope cervicapra (Linnaeus 1758) the Indian blackbuck is the final living antilopine. It is not known from Olduvai but a pair of *Antilope* horn cores has been found below tuff D of the Shungura Formation at Omo.

As a result of the study of material excavated at Olduvai since 1960 there can be considerable modification to the history of the Antilopini in east Africa described by Gentry (1966), although the central conclusion still stands that most of the east African fossils of this tribe are related to *Antidorcas*, now confined to Namibia (South West Africa), South Africa and eastern Botswana, rather than to *Gazella*. From specimens of Antilopini teeth excavated since 1960, especially those in early stages of wear, it now appears that there is only one species of springbok-like antelope in Bed I (cf. Gentry 1966 : 77). Indeed, the amount of variation in horn cores and the levels of occurrence of different varieties suggest that all the Olduvai material, except for one frontlet, is of one species for which the name used hitherto has been *Phenacotragus recki*.

Antilopini have been found at most South African fossil sites. Among them is '*Phenacotragus*' *vanhoepeni* Wells & Cooke (1956 : 43, pls 22–24) known only from Makapansgat Limeworks and now thought to be referable to *Gazella* (Wells 1969b : 162). We concur with Professor Wells' opinion. With this awkward species no longer congeneric with the east African type species of *Phenacotragus*, there seems to be no reason for not sinking the latter genus in *Antidorcas* (cf. Gentry 1966 : 97). This will now be done.

Genus *ANTIDORCAS* Sundevall 1847

1937 *Phenacotragus* Schwarz : 53.

Type species. *Antidorcas marsupialis* (Zimmermann 1780).

Generic diagnosis. Small to moderate-sized antelopes; horn cores of males not usually very compressed, often with transverse ridges, generally diverging strongly from the base or in their distal parts, usually bending backwards a short distance above the base, often more massive basally in relation to their length than in gazelles; frontals hollowed internally and at a higher level between the horn core bases than at the orbital rims; parietofrontals' suture not always complicated; braincase rather short; supraorbital pits small; nasals long; basioccipital with well-marked anterior tuberosities on which the surface rugosity tends to be confined to the anterolateral parts, and with a rather flat appearance of the whole bone behind the anterior tuberosities; upper molars with stronger styles than in *Gazella*; M_3s with a well-developed rearmost (third) lobe; premolar rows shorter than in *Gazella*, with P_2s reduced or absent; mandibular ramus often markedly deepened under the molars.

This genus contains four species in our opinion:

Antidorcas marsupialis, the living springbok,
A. recki (Schwarz 1932), extinct,
A. bondi (Cooke & Wells 1951), extinct,
A. australis Hendey & Hendey 1968, extinct.

Antidorcas recki (Schwarz 1932)

1932 *Adenota recki* Schwarz : 1; pls 1–2.
1937 *Phenacotragus recki* Schwarz : 53; pl. 1, fig. 1.
1949 *Gazella wellsi* Cooke : 38, fig. 11.
1965 'Other gazelles' Leakey : 64(a), (b), (c), (d), (g), (h), (i), HWK II 473 of (j), pls 83–85. Specimens (e) and (k) are indeterminable as no catalogue numbers are given.
1965 *Phenacotragus recki* Leakey : 65; pl. 87.
1965 Reduncini indet. Leakey : 47; pl. 53.
1966 *Gazella wellsi* Gentry : 56; pls 1, 2A and B.
1966 'Other gazelles' Gentry : 64 group A; KK I 1959.309 of pl. 2C.
1966 *Phenacotragus recki* Gentry : 77; pls 5–8.

DIAGNOSIS. A species of *Antidorcas* differing from living *A. marsupialis* in its smaller size; horn cores more mediolaterally compressed and often more sharply bent backwards in their distal parts; ethmoidal fissure present; preorbital fossae less deep posteriorly and possibly larger; basioccipital narrower; teeth smaller; premolar rows less reduced but P_2 sometimes absent at least in later life; upper molars with more concave lateral walls behind the mesostyle; radii, tibiae and metapodials shorter, tibiae with more forward curvature, radii with smaller lateral tubercles proximally. Some populations are without increased divergence of the more distal parts of the horn cores.

HOLOTYPE. A skull with dentitions and the right horn core from Olduvai, formerly in Munich but unfortunately destroyed during the Second World War. A cast of this skull is in London, BM(NH) M 21460, and a cast of the cast is in the Nairobi collections.

HORIZON. According to Dietrich (1933 : 301) the holotype skull came from 'Horizont 4?'. The species is known by numerous horn cores and dentitions from Bed I to Bed IV at Olduvai, and occurs at Kanjera, Peninj, Laetolil and the Omo Shungura Formation. In South Africa it is known from Bolt's Farm, Elandsfontein and the Vaal River gravels.

REMARKS. Remains of *A. recki* in London are a herd excavated from SHK II in 1935 consisting of at least eleven mostly immature individuals (Gentry 1966 : 77); a right horn core M 22360 from DK I in 1935; left horn core M 14513 from Bed I in 1931; right horn core M 14509 from Bed I in 1931; cranium with the bases of both horn cores M 22365 from VEK I; two right horn cores, M 14510 and M 14512, found in Bed I in 1931; left horn core M 14511 from Bed I in 1931; right horn core M 22363 from Bed I in 1947; base of a left horn core M 22479 from Bed I; left horn core M 21457 from VEK I in 1935, the 'Mongolian gazelle' (Leakey 1965 : 64(b)), considered as possibly a small *Damaliscus* or related genus by Gentry (1966 : 104); left horn core M 21456 found on the surface of VEK II in 1935; distal half of a left horn core M 22361 from VEK II in 1935; cranium with horn cores M 21463 from the surface of FLK II in 1935 (Leakey 1965 : 64(d), pl. 85, which is not M 21462 from VEK I in 1931 as stated); left female horn core

M 22362 from FLK II in 1935; the medial basal part of a right horn core M 14565 from Bed IV in 1931; right horn core M 14563 from VEK IV.

Characters of the face of *A. recki* are known from the cast of the holotype skull and partly from the two Nairobi specimens FLKN I 6334 and FLKN I 7266 (Pl. 39, fig. 4). The small frontlet with horn core bases in Nairobi, FLKN I 1039, figured as Reduncini indet. by Leakey (1965 : 47, pl. 53), is here identified as *A. recki.*

Most horn cores of this species from Bed I agree well with *Gazella wellsi* Cooke, according to an unpublished paper by Dr H. B. S. Cooke on the South African Bolt's Farm site in which he deals with specimens more complete than the holotype mandible from the Vaal River gravels and supposedly conspecific with it. *G. wellsi*, as there understood, is characterized by horn cores that are bent back sharply near the base, fairly strongly divergent from the base in anterior view but without sharp outward divergence of the distal part, with a flattened lateral surface, little transverse compression, a tendency to a posterolateral edge and well-marked transverse ridges on the anterior surface.

The London herd was referred to *Phenacotragus recki* Schwarz by Gentry (1966 : 77). The barely adult cranium BM(NH) M 21464 (Leakey 1965 : pl. 83; Gentry 1966 : pl. 5A–B) and older frontlet M 21462 (Leakey 1965 : pl. 84 which is not M 21463 as stated in the caption; Gentry 1966 : pl. 5C–D) have horn cores which differ from those in Bed I by being longer, more nearly parallel at the base in anterior view and then diverging more in their distal parts, more symmetrical in cross-section and without a flattened lateral surface. The horn cores of the London cast of the *P. recki* holotype, M 21460, agree in these features except that they are less nearly parallel at the base and rise further before bending backwards.

The extensive variation among *A. recki* horn cores weakens any simple concept of different horn core types in successive horizons at Olduvai. Besides the commonest sort of Bed I '*Gazella wellsi*' horn core already described, there are at least four other sorts from horizons below the Lemuta Tuff. One, represented by horn cores KK I 1959.309, BM(NH) M 14512 from Bed I, HWK II 1959.472, HWK EE II 1972.2780 and HWK EE II 1972.3108 differs by being more strongly compressed and having a less clearly flattened lateral surface. The HWK II horn core is much smaller than the others and might be a female or perhaps a small male. Another variety, represented by horn core 1960.067/250 from FLKN I level 5 is more divergent distally, has less pronounced backward bending and is definitely without a flattened lateral surface. Yet another, represented by horn cores FLKN I 8659 from levels 1 to 2 and FLKN I 8194 from level 5 (which is associated with antilopine postcranial bones), has strong mediolateral compression, an almost regular oval cross-section and an evenly increasing degree of backward curvature in side view. A fourth sort, represented by horn core BM(NH) M 22360 from DK I in 1935, is narrowed anteriorly but this is only a small difference. We do not know that the sort of horn core which happens to have become most commonly fossilized in these horizons at Olduvai is more typical of the species than the other varieties. Horn cores with many Bed I '*Gazella wellsi*' features may come from deposits later than the Lemuta Tuff, examples being the horn core BM(NH) M 14563 supposedly from Bed IV, and probably the Bolt's Farm material. These later horn cores are our main reason for not founding two chronological subspecies for those *A. recki* specimens occurring before and after the Lemuta Tuff. Also, the horn cores BK II 1955.71 and BM(NH) M 14513 from Bed I at Olduvai, BM(NH) M 15862 from Kanjera, A67.256 and A67.257 (WN64.113) from Peninj constitute yet another (mainly later than Bed I) morphological variety within *A. recki*; they are short and taper rapidly to a point from their thick bases, and have no flattened lateral surface or transverse ridges. Horn cores from other sites in Africa may well show still further variations in morphology. In these circumstances all we can say is that the majority of Olduvai Bed I and lower Bed II horn cores show no distal divergence, but most of those from later levels do.

The question of which horn cores, if any, represent the females of *A. recki* is still unsolved. The former concept of Gentry (1966 : 79) about possible female horn cores cannot be maintained. It is now certain that variation among the Olduvai horn cores is too complicated to permit the clear separation of two sexual types. A possible female would be BM(NH) M 22362, erroneously taken by Gentry (1966 : 65, pl. 7A) as a female of the Olduvai *Gazella* species. The horn core

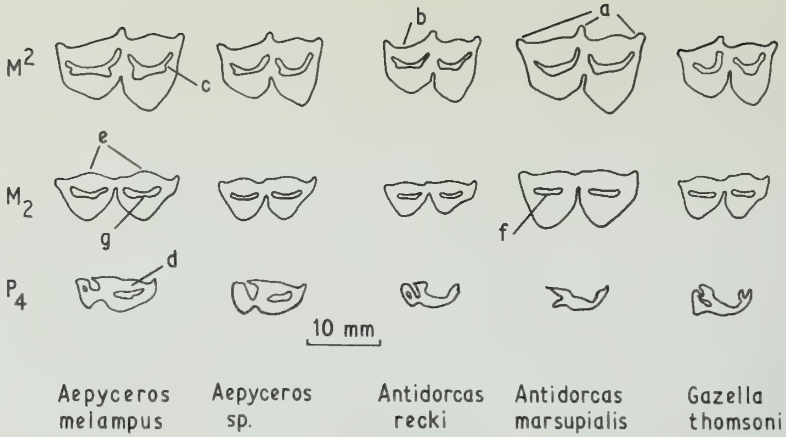


Fig. 32 Occlusal views of teeth of *Aepyceros* and Antilopini. All teeth are of the right side, and the anterior direction lies to the right. *Aepyceros* sp. is from the Shungura Formation, members B to G.

pedicel is hollowed, which fits *Antidorcas*, and there is very little backward bending. The only acceptable alternative to M 22362 as a female is to assign the more slender but otherwise normal horn cores, for example FLKN I 6334 and HWK II 1959.472, to the female sex. At present we are undecided which is the correct solution.

As a result of seeing South African fossil antilopine material and the abundant earlier impala from Omo, we can revise the list of tooth differences given by Gentry (1966 : 96) for distinguishing *Antidorcas* teeth from those of *Gazella* and *Aepyceros* (Fig. 32, a–f):

1. The styles on upper molars are strong in living and fossil *Antidorcas* and *Aepyceros*; they are less pronounced in living *Gazella*, but the Makapansgat Limeworks *G. vanhoepeni* does not differ appreciably from *Antidorcas* (a).
2. A concave posterior part of the lateral wall of upper molars is frequent in fossil *Antidorcas*, *G. vanhoepeni* and living and fossil *Aepyceros*; this is linked with the strength of the mesostyle and therefore with the previous character (b).
3. A tendency to complicated central cavities is found in living and fossil *Aepyceros* upper molars (c).
4. Paraconid–metaconid fusion to close the anterior part of the medial wall of P_4 occurs only in *Aepyceros* (d).
5. There is possibly more outward bowing of the medial walls of lower molars of living *Aepyceros* (e).
6. Central cavities on the lower molars become straight late in wear in *Antidorcas* and some *Gazella*; in *Aepyceros* they often appear constricted centrally and straightening does not occur in late wear (f).
7. M_3 may be relatively longer in later wear in *Antidorcas*.
8. Premolar reduction is carried further in *Antidorcas* than in *Gazella* and *Aepyceros*. It is especially pronounced in *Antidorcas marsupialis*.
9. Deepening of the horizontal ramus beneath the molars is noticeable in most *Antidorcas* (but not, for example, in the majority from Olduvai Bed I).

Thus the differences between the fossil teeth of *Antidorcas* and *Gazella* are few, and at a time level such as the Shungura Formation of Omo it is hard even to distinguish *Aepyceros* teeth.

A large number of limb bones of *Antidorcas recki* have been excavated from Bed I, Olduvai. The tibiae, radii and metapodials are shorter and thicker than in living Antilopini, and there is no sign of the very long metatarsals characteristic of living springbok (Fig. 33).

MEASUREMENTS. Measurements on the crania of *A. recki* are:

	VEK I M 22365	SHK II M 21464	FLK II M 21463	M 21460 (cast)
Skull width across posterior side of orbits	–	85.2	–	94·6
Length of horn core along its front edge	–	129·0	–	–
Anteroposterior diameter of horn core at its base	–	30·6	29·5	37·4
Mediolateral diameter of horn core at its base	–	24·6	24·0	30·7
Minimum width across lateral surfaces of horn core pedicels	–	59·0	65·8	–
Width across lateral edges of supraorbital pits	–	30·6	33·4	30·2
Length from back of frontals to top of occiput	63.3	59·8	–	–
Length from midfrontal suture at the level of the supraorbital pits to top of occiput	95·3	93·2	–	97·6
Maximum braincase width	–	*c.* 51·7	–	64·5
Skull width at mastoids immediately behind external auditory meati	–	57·1	–	73·3
Occipital height from top of foramen magnum to top of occipital crest	–	22·9	–	–
Width of anterior tuberosities of basioccipital	23·4	17·0	–	–
Width of posterior tuberosities of basioccipital	29·0	23·2	–	–
Occlusal length P^2–P^4	–	–	–	23·3

Measurements on two frontlets of *A. recki* are:

	FLKN I 1039	SHK II M 21462
Skull width across posterior side of orbits	101·0	92·0
Length of horn core along its front edge	–	*c.* 177·0
Anteroposterior diameter of horn core at its base	35·2	33·8

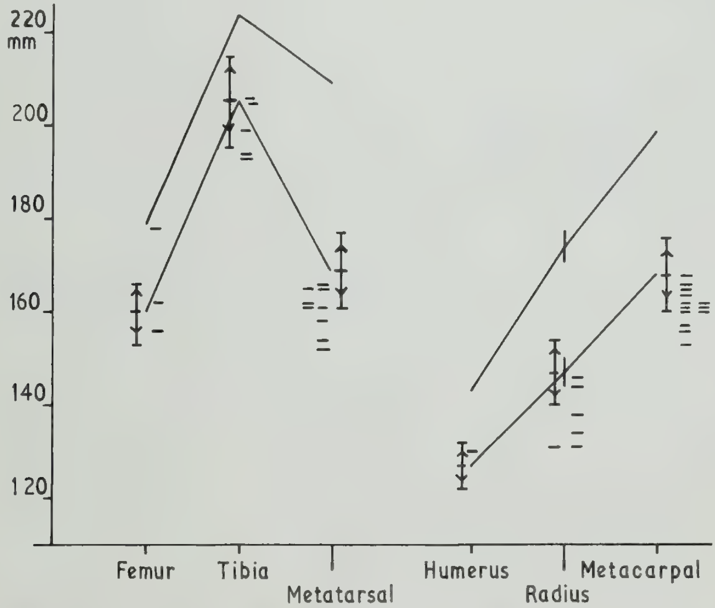


Fig. 33 Lengths of limb bones in Antilopini. The upper line is the mean of 6 *Antidorcas marsupialis*, and the lower of 14 *Gazella thomsoni*. Ranges and standard deviations have been added for the latter. Horizontal dashes indicate antilopines from Bed I, Olduvai Gorge.

Mediolateral diameter of horn core at its base	27·2	25·6
Minimum width across lateral surfaces of horn core pedicels	66·4	61·3
Width across lateral edges of supraorbital pits	–	30·0

Anteroposterior and mediolateral diameters at the base of horn cores of *A. recki*, followed by their length, are:

DK I BM(NH) M 22360	34·9 × 25·0
THC I 068/6659	32·7 × 24·9
FLK I G.229	32·4 × 26·7, length 153·0
FLKN I 1307	34·7 × 23·3, length 140·0
FLKN I 6334	30·2 × 23·7, length 140·0
FLKN I 7266	33·4 × 27·9, length 140·0
FLKN I 067/250	31·5 × 23·3, length 153·0
VEK I BM(NH) M 21462	33·8 × 25·6
VEK I BM(NH) M 21457	33·7 × 24·8
KK I 309	30·9 × 22·1
Bed I BM(NH) M 14509	30·2 × 21·5
Bed I BM(NH) M 14511	31·2 × –
Bed I BM(NH) M 14512	30·1 × 21·2
Bed I BM(NH) M 22363	33·4 × 26·3
HWK II 471	31·2 × 24·6
HWK II 472	22·3 × 16·3
HWK II 568	32·4 × 25·5, length 140·0
HWK East II 278	24·8 × 20·8, length 133·0
HWK EE II 2780	30·9 × 21·3, length 137·0
HWK EE II 3108	25·1 × 17·5, length 119·0
Long K West II 068/6657	30·4 × 24·0, length 140·0
VEK II surface BM(NH) M 21456	34·0 × 29·0
FLK II BM(NH) M 22362	17·8 × 14·9
BK II 1955.71	32·5 × 25·9
VEK IV BM(NH) M 14563	38·1 × 28·2

Measurements on an associated maxilla and mandible of *A. recki* from FLKN I are:

Maxilla 7266		Mandible 7284	
Occlusal length M^1–M^3	36·3	Occlusal length M_1–M_3	39·9
Occlusal length M^2	13·6	Occlusal length M_2	12·6
Occlusal length P^2–P^4	21·0	Occlusal length P_2–P_4	–

These belong to the same individual as the horn core FLKN I 7266 whose measurements are given above.

Measurements on four maxillae of *A. recki* from FLKN I are:

	627	7555	10286	1662
Occlusal length M^1–M^3	38·4	40·1	37·6	46·8
Occlusal length M^2	13·8	14·2	12·1	16·1
Occlusal length P^2–P^4	19·0	–	–	23·4

Maxilla 1662 is rather large and may be another species.

Measurements on 10 mandibles of *A. recki* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_1–M_3	8 (left + right)	41·8	36·7–46·5	3·6	1·28
	5 (right only)	42·7	39·9–46·0	2·5	1·13
Occlusal length M_2	9 (left + right)	12·8	11·1–14·8	1·3	0·43
	5 (right only)	13·4	11·8–14·8	1·2	0·54

Measurements on mandibles of *A. recki* from FLK I are:

	D.35	B.119	G.154	G.294	G.323	B.492
Occlusal length M_1–M_3	43·5	–	–	42·5	47·2	43·5
Occlusal length M_2	11·7	13·1	13·1	11·9	14·5	11·4
Occlusal length P_2–P_4	–	19·1	18·7	13·2 (P_3–P_4)	–	–

Measurements on two other mandibles of *A. recki* are:

	DK I 261	HWK East II 2103
Occlusal length M_1–M_3	42·8	42·5
Occlusal length M_2	13·7	12·9
Occlusal length P_2–P_4	19·5	–

Immature mandibles FLKN I 231, FLKN I 1310 and FLKN I 7828 have deciduous P_2–P_4 measuring 22·5, 26·7 and 27·2 mm respectively.

Measurements on 16 metatarsals assigned to *A. recki* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length	16 (left + right)	164	152–185	7·3	1·84
	9 (left only)	163	152–185	9·6	3·21
Least thickness	16 (left + right)	11·5	10·3–12·8	0·5	0·14
	9 (left only)	11·3	10·3–11·7	0·5	0·15

Measurements on 19 metacarpals assigned to *A. recki* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length	19 (left + right)	161	153–168	4·2	0·98
	13 (left only)	161	153–168	4·2	1·17
Least thickness	19 (left + right)	12·9	11·6–15·1	0·8	0·19
	13 (left only)	13·0	11·6–15·1	0·8	0·22

Measurements of length and least thickness on other limb bones assigned to *A. recki* are:

Femora	DK I 3330	162 × 15·4	DK I 5385	178 × 16·0		
Tibiae	DK I 4366	205 × 14·5	FLK I 9	211 × 16·4	FLK I F.161	206 × 15·7
	FLKN I 157	193 × 14·5	FLKN I 1246	199 × 15·6	HWK East II 2010	202 × 16·3
Metatarsal	DK I 3292	165 × 10·9				
Humeri	FLKN I 8191	130 × 14·4	FLKN I 10263	130 × 15·1		
Radii	FLKN I 50	141 × 18·1	FLKN I 70	138 × 16·8	FLKN I 666	146 × 16·3
	FLKN I 682	144 × 17·9	FLKN I 1300	134 × 16·2	FLKN I 1605	131 × 16·0
	FLKN I 8179	137 × 16·6	BK II 1963.3037	157 × 16·6		
Metacarpal	FLKNN I 649	162 × 11·7				

Associated tibia FLKN I 8264 194 × 14·2 and metatarsal FLKN I 8263 161 × 11·3 mm.

COMPARISONS. Four Laetolil horn cores in Berlin of *Gazella hennigi* Dietrich (1950 : 25; pl. 1, figs 1–2) agree in size and morphology with the shorter horn cores of *Antidorcas recki* (see p. 429 above). They differ from those of the common *G. janenschi* Dietrich (1950 : 25; pl. 2, fig. 22) by tapering more quickly, curving back more strongly and diverging quite strongly in their upper parts. The horn core from the Garussi water course is uncompressed, but two from Gadjingero, 45 and 3.39, and one from the Vogel River labelled 'Vo 330 *G.* sp. cf. *capricornis*', are compressed. Dietrich's illustration of the right horn core 45 from Gadjingero is slightly larger than life size.

Scarce horn cores and dentitions from the Shungura Formation, Omo, are of *A. recki* or its progenitor. The horn cores come from levels above Tuff F and differ from the Olduvai Bed I horn cores by a less sharp bending backwards of their distal part, but they do show a flattened lateral surface, transverse ridges and lack of increased divergence in the distal part. An *Antidorcas* mandible is known from member B, but other dental remains are limited to member G. The Omo mandible referred to *Antidorcas* sp. by Arambourg (1947 : 390; pl. 30, fig. 3) is most probably an alcelaphine, as has been mentioned on p. 420.

The right and left horn core bases at Peninj, A67.256 and A67.257 (WN64.113), mentioned on p. 429 above, are also *A. recki*. Both sides of a complete upper dentition A67.274 (WN64.300B.2 PT 3.USC), part of a right mandible A67.280 (WN64.241.TMG S.5.?BSC), part of a left mandible A67.296 (WN64.95.MMG.BSC), a left lower molar A67.315 (WN64.152.RDG.S) and a deciduous left P_4 A67.281 (WN64.291.PP.USC) may be the same species. There is no evidence for more than one *Antidorcas* species at Peninj (cf. Gentry *in* Isaac 1967 : 254).

At Kanjera the left horn core BM(NH) M 15862, already mentioned, represents *A. recki*. It was identified as *Phenacotragus recki* by Hopwood (*in* Kent 1942 : 126). A distal left tibia M 22500 and distal left humerus M 22499 could also belong to *A. recki*.

Several Elandsfontein fossils agree with the *Antidorcas recki* horn cores from Bed I in the transverse ridges on the front surface and lack of increased divergence in the upper parts, but lack a flattened lateral surface and are less mediolaterally compressed. These fossils are a frontlet 8542, right horn core 1195, left horn core 20587 and part of a horn core 6750. They differ from living *A. marsupialis* horn cores in having transverse ridges, no increased divergence in their distal parts, and the backward bend being closer to the base.

Other fossil *Antidorcas* at southern African sites, however, are not conspecific with the east African *A. recki*. Almost certainly to be included in *Antidorcas* is *Gazella bondi* Cooke & Wells (1951 : 207, fig. 3) founded on material from Chelmer, Rhodesia, with an immature row of left upper teeth as holotype. The teeth were smaller than those of impala, had strong styles and were extremely hypsodont. Similar small and very hypsodont teeth from Vlakkraal had been referred to *Antilope* gen. et sp. indet. by Wells, Cooke & Malan (1942 : 217), and Cooke (*in* Mason 1962 : 452) listed the species for Middle Stone Age levels of the Cave of Hearths. Three mandibles at Florisbad (all numbered C.1473) and a large number of isolated teeth are apparently of this species and have typically antilopine moderate-sized to large back lobes on M_3, a springbok-like short premolar row with even P_3 suffering reduction, and a mandibular ramus deepening considerably under the molars. Like the type specimen from Chelmer, all these *bondi* remains are of immature animals. Nevertheless, the immature mandibles of the SHK II herd of *A. recki* definitely have less hypsodont teeth than '*Gazella*' *bondi*, and we would regard this difference in tooth development as more reliable than insubstantial variations in horn core morphology. Vrba (1973) has published an account of cranial remains of *A. bondi* from Swartkrans. The horn cores from this site are less mediolaterally compressed than in other *Antidorcas*, diverging more at the base than higher up and with a tendency to an anticlockwise torsion on the right side, and without a sharp backward bend in their course. The supraorbital pits are rather large for an *Antidorcas*. Despite these very distinctive features, the cranial and basioccipital characters are very like *A. recki* (Vrba 1973 : 290). Vrba also draws attention to some further interesting tooth characters: the lower molars having little flattening of their medial walls, their central cavities with transverse constrictions in the middle, the small occlusal area of the cheek teeth (figs 2, 6) and the extreme shortness of the premolar row (fig. 7). It is unlikely that *A. bondi* was ancestral to *A. marsupialis*. Further discoveries may allow us to know whether its horn core morphology was as variable as that of *A. recki*.

The holotype of *Gazella wellsi* Cooke (1949 : 38, fig. 11) is a left mandible F262 from the Vaal River gravels of Power's site. It is housed in the Department of Archaeology, University of Witwatersrand, Johannesburg. It remains questionable whether this name-bearing mandible is conspecific with *A. recki* or with *A. bondi*, but the stability of the older name *A. recki* will not be affected. Measurements on this mandible are:

Occlusal length M_1–M_3	43·6	occlusal length M_2	13·3

An interesting springbok, *Antidorcas australis*, was described from Swartklip, Cape Province (Hendey & Hendey 1968 : 56, pls 3–4; Hendey 1974 : 52). There are several complete and partial crania and dentitions, which differ markedly from the living springbok by having smaller horn cores which are more mediolaterally compressed and which lack the sharp bending backwards and outwards shortly above the base. They thus have some resemblance to the much smaller female horn cores of living springbok. The dentitions at Swartklip are also smaller. *A. australis* has been recorded from Melkbos (Hendey 1968 : 111), and is also known from Elandsfontein by frontlets 8860, 12214A, 20564 and many horn cores—far more than of *A. recki* at that site. Hendey (1974 : 52) believes that *A. recki* may have been more a species of inland plateaux, and that it is a more likely ancestor for *A. marsupialis* than is *A. australis*. Vrba (1973 : 300) has assigned some Swartkrans horn cores to *A. australis*, and believes that some Swartkrans dental remains are conspecific.

Horn cores of *Antidorcas marsupialis* are known from Florisbad (C.1459 A and B, C.1469), and there are a few springbok-like teeth larger than those of *A. bondi* at the site. One wonders if they come from the same low level as the rest of the fauna and particularly the *A. bondi*.

Antidorcas, or a closely related genus, has been claimed to occur in the north African

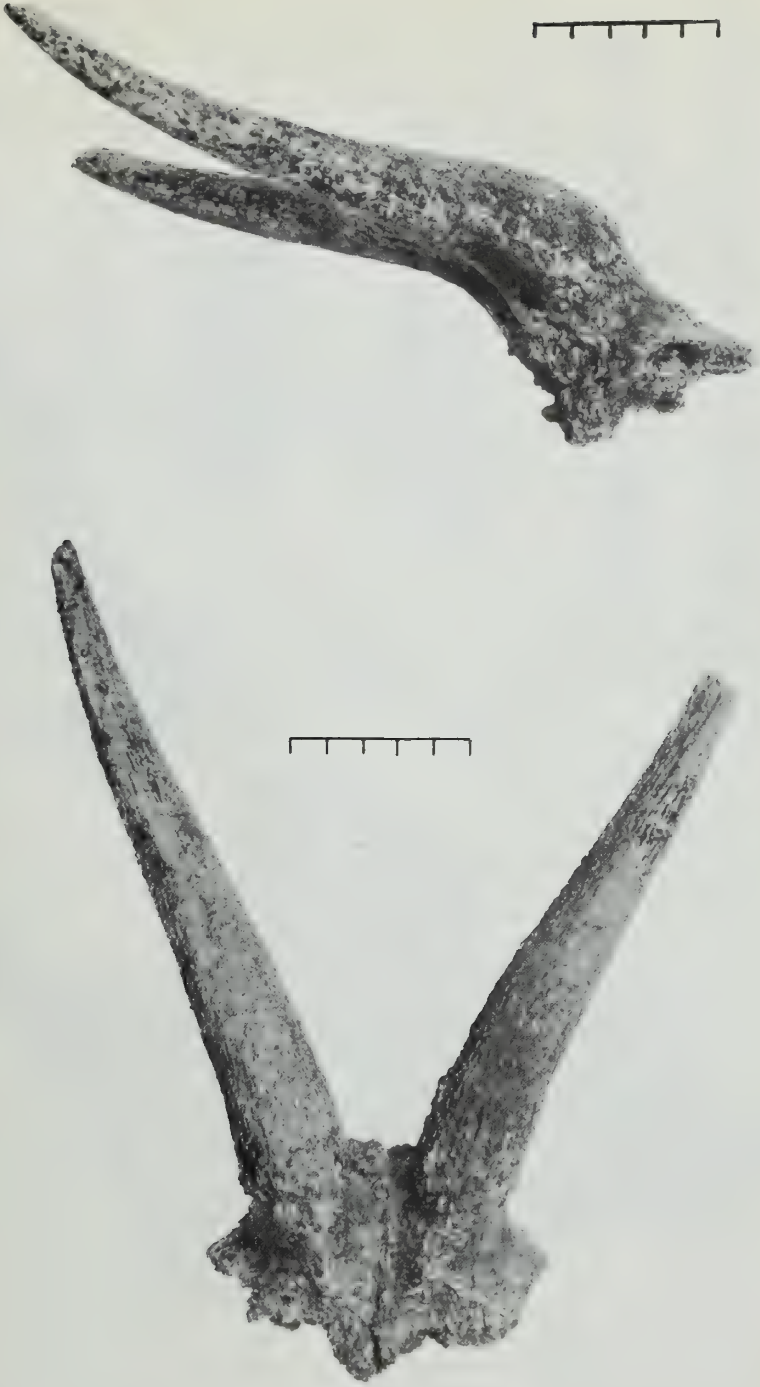


Plate 38 (Scales marked in centimetres)

Antidorcas sp. Lateral and dorsal views of frontlet, HEB East IV 1969.814.

Villafranchian-equivalent deposits of Ain Brimba, Tunisia, and Ain Boucherit and Oued el Atteuch, Algeria (Arambourg & Coque 1958 : 612; Coppens 1971 : 53). Bayle (1854) had earlier referred to what may be the same species from Mansoura, Algeria.

Leakey (*in* Clark 1959 : 230) identified as *Litocranius* sp. most of a poorly preserved right tibia BM(NH) M 12150, and proximal and distal right femoral pieces M 12843 and M 12844, from Broken Hill, Zambia. In the more or less central position of the longitudinal digital flexor ridge on its posterior surface the tibia is unlike some species of *Gazella* but does not appear to be especially characteristic of *Litocranius*. The extent of the cnemial crest and its pronouncedly concave lateral surface suggest *Antidorcas* or *Gazella* rather than *Litocranius*. The two femoral pieces are definitely antilopine, but the pit for the origin of the lateral femorotibial ligament can be clearly seen: it is absent in *Litocranius*. The rounded top edge of the great trochanter of the proximal femur may be more like *Litocranius*, but the extent to which this feature may have arisen from superficial damage is uncertain. An unregistered antilopine distal end of a metacarpal, not mentioned by Leakey, has the small indentations above the condyles on the anterior surface probably too deep for *Litocranius*. M 12872 is the distal end of a left antilopine humerus. Although the identification of all these small limb bones is not secure, they seem more likely to indicate *Antidorcas* or *Gazella* than *Litocranius*.

Antidorcas sp.

An *Antidorcas* frontlet from Bed IV with complete right and nearly complete left horn cores and the dorsal parts of both orbital rims, HEB East 814 found in 1969 (Pl. 38), differs from Bed II fossils of *A. recki* in being a little larger, and in having horn cores which bend backwards less strongly and nearer the base and are less mediolaterally compressed. It could belong to *A. recki*, which is represented in Bed IV, or it could be an early *A. marsupialis*. Further finds from Bed IV will be necessary before coming to a decision.

The measurements of this specimen are:

Length of horn core along its front edge	200·0
Anteroposterior diameter of horn core at its base	37·4
Mediolateral diameter of horn core at its base	30·6
Minimum width across lateral surfaces of horn core pedicels	71·7
Width across lateral edges of supraorbital pits	*c.* 39·0

Genus ***GAZELLA*** Blainville 1816

TYPE SPECIES. *Gazella dorcas* (Linnaeus 1758).

GENERIC DIAGNOSIS. Horn cores subcircular or elliptical in cross-section, with some mediolateral compression, the lateral surface often flatter than the medial, fairly uprightly inserted with backward curvature in side view, generally more obliquely set in females than in males of the same species, slightly divergent in anterior view, without keels or torsion; frontals without or almost without internal sinuses and the area between the horn core bases hardly raised above the level of the top of the orbital rims; moderately large triangular supraorbital pits at the base of the horn core pedicels slightly medial to the anteriormost edge of the pedicels; ethmoidal fissure present; moderate to large preorbital fossae; premaxillae generally contacting the sides of the nasals which have shortened during evolution; occipital low with each half often facing partly laterally as well as backwards; moderate to large auditory bullae; living species with hypsodont teeth but less hypsodont in earlier fossil species; upper molars with moderately prominent styles and little development of ribs between them; lower molars without goat folds; M_3s often with the rearmost (third) lobe greatly enlarged; except in the east Asian subgenus *Procapra*, P_4s are without metaconid–paraconid fusion to form a complete medial wall at the front of the tooth.

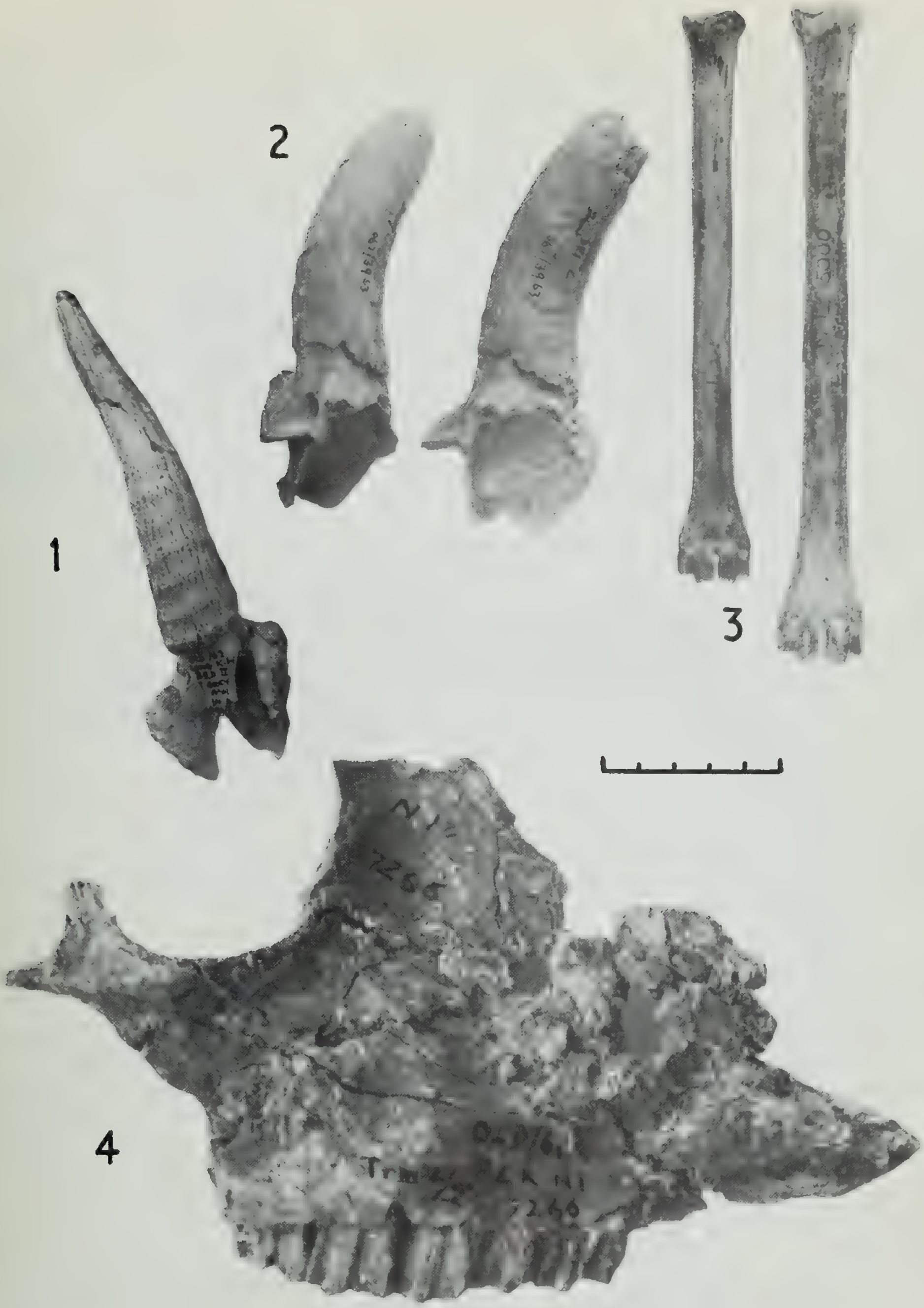


Plate 39 (Scale = 50 mm for Figs 1–3 and 25 mm for Fig. 4)

Antilopini

Fig. 1 ***Antidorcas recki.*** Anterior view of right horn core, Long K West II 1962.068/6657.

Fig. 2 **Antilopini** sp. 1. Anterior and lateral views of left horn core, DK I Surface 1962.067/3963.

Fig. 3 Anterior views of left metatarsals, FLKN I 9372 (left) and FLKN I 5000 (right).

Fig. 4 ***Antidorcas recki.*** Right side of face, FLKN I 7266, to show the preorbital fossa.

Gentry (1966 : 64–67) arranged the *Gazella* horn cores from Olduvai in two groups: **(1)** SHK II 1953.285, BK II 1955.218 + 226, a tip KK II 1959.224, BM(NH) M 14507 from Bed I, and two female horn cores KK I 1959.310 and BM(NH) M 22362 from FLK II all showed little mediolateral compression; **(2)** M 14508 from Bed I was more compressed.

A few additional *Gazella* have now come to light. These are the base of a right horn core EF-HR 1963.199 with the frontal, midfrontal suture, supraorbital pit and damaged orbital rim from middle Bed II, an incomplete right horn core FC West 1963.201 with the top of the orbital rim, supraorbital pit and postcornual fossa also from middle Bed II, a complete right horn core HWK EE 1972.2396 with the midfrontal suture, supraorbital pit, postcornual fossa and damaged orbital rim from lower middle Bed II, a left horn core base BM(NH) M 26929 collected in 1931 possibly from Bed I, and a right horn core 068/6695 with the orbital rim and midfrontal suture. Mrs M. D. Leakey (personal communication) thought that the last fossil might come from Bed I and have adherent matrix from a later deposit. R. L. Hay (personal communication, September 1973) wrote: 'The matrix is a slightly clayey quartzose sandstone with a few percent each of augite and altered volcanic glass of probable original basaltic composition. This is a common type of sandstone throughout the western exposures (Main Gorge, west of FLK) of Bed II above the disconformity at the top of the Lemuta Member. This type of sandstone is rare in any other stratigraphic unit at Olduvai.'

It can be seen from the measurements and Fig. 34 that the extent of mediolateral compression in Olduvai *Gazella* horn cores is greater than can be expected in a single species, but that M 14508 is scarcely more compressed than M 14507, FC West 201 or HWK EE 2396. The last is very like the middle and upper Bed II horn cores but thinner mediolaterally. We now take the horn cores as being of one unnamed species, with M 14508 only doubtfully included. The female horn core M 22362 has internally hollowed frontals and can no longer be accepted as belonging to *Gazella*

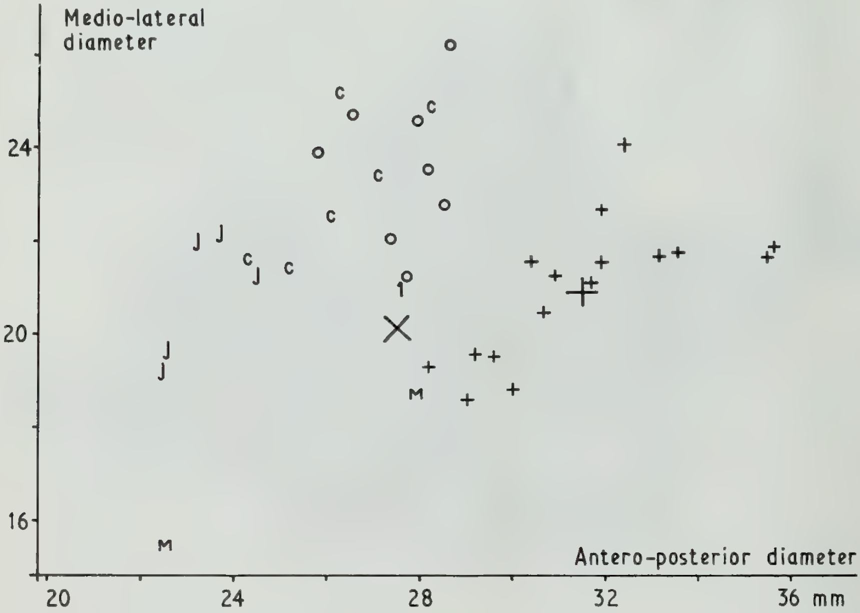


Fig. 34 Horn core dimensions of gazelles.

O = *Gazella* sp. from Olduvai and Peninj, C = same species from Elandsfontein, J = *Gazella janenschi* from Laetolil, M = *G. praethomsoni* from the Shungura Formation, 1 = BM(NH) M 14508; the adjacent circle is *Gazella* sp. HWK EE 2396, + = *G. thomsoni*, with a large + indicating the mean reading, large X = mean for 13 *G. dorcas*.

(see p. 429). The remaining horn cores can be described as moderately long, slightly divergent, inserted rather obliquely, only a little curved backwards, without transverse ridges, having a flattened lateral surface, often with deep longitudinal grooving anteriorly and posteriorly, and having the greatest mediolateral diameter situated nearly centrally on the cross-section. The postcornual fossae are variably deep, as in living gazelles, but often more strongly localized. There is no internal hollowing of the frontals at the horn core bases, and the level of the frontals between the horn cores is no higher than the orbital rims.

The gazelle mandibles SHK II 1957.793, BK II 1952.152 and a surface find from MLK II in 1955 can also be placed in this species, as was done by Gentry (1966 : 66). We can thus be sure that a gazelle with little-compressed horn cores occurs in Olduvai middle and upper Bed II. It probably also occurs in Bed I, but at that time its horn cores were a little more compressed.

Leakey (1965 : 64) provisionally used the name *Gazella praecursor* Schwarz for the horn cores M 14507 and M 14508. Schwarz (1937 : 41; pl. 2, figs 4–5) had founded *G. gazella praecursor* on Olduvai material, which was destroyed in the Second World War. Unfortunately he figured only a tibia and a cervical vertebra, and described the horn cores as very compressed, parallel proximally but diverging outwardly in their upper parts, and with the upper parts strongly bent backwards. To us this reads more like a description of *Antidorcas recki* than of *Gazella* horn cores, although we have not taken the step of formally listing *G. g. praecursor* as one of the synonyms of that species. We believe the name *G. g. praecursor* should be dropped from use.

Measurements. Anteroposterior and mediolateral diameters at the base of the gazelle horn cores are:

Bed I BM(NH) M 14507	27·4 × 22·0	HWK EE II 1972.2396	27·7 × 21·2
Bed I BM(NH) M 14508	27·6 × 21·0	SHK II 1953.285	28·7 × 26·2
Bed I? BM(NH) M 26929	28·0 × 24·6	BK II 1955.218 + 226	26·6 × 24·7
FC West II 1963.201	28·6 × 22·8	068/6695	28·2 × 23·5

The length along the front edge of SHK II 1953.285 is 160·0, and of HWK EE II 1972.2396 153·0 mm.

Measurements on the gazelle mandibles are:

	SHK II 1957.793	BK II 1952.132
Occlusal length M_1–M_3	40·4	–
Occlusal length M_2	13·0	13·2
Occlusal length P_4	9·6	–

Comparisons. The gazelle of Olduvai middle and upper Bed II is represented at Elandsfontein by a number of horn cores, including 9473. Some very small straight ones are the females, for example 3783, 12753 and 16522. Some mandibles, for example 2855 with a complete row of cheek teeth, can also be attributed to the species. The only other site from which we know the species is Peninj, on the evidence of the right horn core A67.248 (WN64.75 MMG/N). The anteroposterior and mediolateral diameters at the base of this horn core are 25·8 × 23·9 mm.

This Olduvai, Elandsfontein and Peninj gazelle differs from both *G. dorcas* and *G. thomsoni* in its less compressed horn cores and relatively longer premolar rows. However, the level of the greatest mediolateral diameter lies more anteriorly on the cross-section than in *G. dorcas* and this does not differ from *G. rufifrons* and *G. thomsoni.* The low inclination of the horn cores is a further resemblance to the two latter species, so we may tentatively align the fossil species more closely with them than with *G. dorcas.*

Among named fossil forms *G. praethomsoni* Arambourg (1947 : 387; pl. 32, figs 4, 4a) from Omo is characterized by extreme mediolateral compression of the horn core, and is certainly a distinct species from the Olduvai middle and upper Bed II gazelle. A second and larger horn core, L.35–35, was found in 1968 in member G of the Shungura Formation. A still larger and strongly curved complete horn core, B.377 from the Brown Sands locality of the Usno Formation, may also be the same species. It seems likely that these horn cores represent a different lineage from the Olduvai gazelle, and did not evolve into that species by lessening their horn core compression.

Despite Arambourg's choice of a specific name and the mediolateral compression of its horn cores, *G. praethomsoni* need not be ancestral to *G. thomsoni*. The closest relative of the latter must surely be the west African *G. rufifrons* with its less compressed horn cores, and this makes the Olduvai gazelle equally available as an ancestor. The mandible which Arambourg (1947: pl. 27, figs 1, 1a and 1b) assigned to *G. praethomsoni* is from an antilopine, perhaps *Antidorcas*.

Another named African fossil gazelle is *G. gracilior* Wells & Cooke (1956 : 37; pls 20–21) from Makapansgat Limeworks. The holotype frontlet BPI M.773 was described as the male of a small slender-horned gazelle, but the small horn cores set so widely apart suggest that it could equally well be the female of a larger species. The London specimen figured by Wells & Cooke, BM(NH) E.5775 (Anthropology collection), is more robustly horned but the postcornual fossa lies somewhat laterally to the horn core base instead of being tucked up near it as would be normal in a male gazelle, which suggests that this fossil is also a small-horned, presumably female example of a larger species. The braincase wall behind the horn core projects quite a long way laterally. The lack of any flattening of the lateral surface of the horn core or of deep longitudinal grooving anteriorly or posteriorly, and the smooth texture of the surface are also compatible with it being a female. The mandibles assigned to *G. gracilior* (BPI M.766, M.767, M.768 and M.771) by Wells & Cooke are all rather large. In fact, all the *G. gracilior* material from Makapansgat Limeworks probably belongs to *G. vanhoepeni* (see p. 443).

A multitude of specific names already exists for north African fossil gazelles. Arambourg (1957) has brought some order to those of the upper Pleistocene, but his final opinions on the Pliocene and earlier Pleistocene ones have yet to appear. It can be accepted that a gazelle for which *G. atlantica* Bourguignat (1870 : 84; pl. 10, figs 14–15) is the correct name was abundant in the middle and later Pleistocene of Barbary. It was moderately large, about the size of a springbok, and had rather short and thick horn cores showing little mediolateral compression, strong backward curvature and a flattened lateral surface. The supraorbital pits were sometimes large, and the basioccipital of a male cranium seen by A. W. Gentry in Paris some years ago had poorly marked anterior tuberosities situated closer together than in living gazelles. Despite its short and backwardly-curved horn cores *G. atlantica* is probably not related to *G. dama* because it is no bigger than contemporaneous fossils of *G. cuvieri*, whereas *G. dama* is a much bigger species. On the other hand *G. dorcas* is rather small to be descended from *G. atlantica*. Bate (1940 : 419, 429) described gazelles of a size close to *G. atlantica* from the early Holocene of Palestine. For the present the identity of these gazelles is best left open, and we may merely note that the Olduvai gazelle is unlikely to be *G. atlantica* on account of its smaller size, longer horn cores with weaker backward curvature, and perhaps the smaller supraorbital pits.

G. tingitana Arambourg (1957 : 68; pl. 1, figs 1–4; pl. 2, figs 6, 8) is a late Pleistocene north African species having long slender horns like the living *G. leptoceros* but more backwardly curved. Other middle and later Pleistocene fossils from this area can be assigned to living species, so none are like the Olduvai gazelle.

Two names exist for north African horn cores of an age equivalent to the Villafranchian. One is *G. setifensis* (Pomel 1895 : 15; pl. 10, figs 14–15), and the other *G. thomasi* (Pomel 1895 : 18, a renaming of '*G. atlantica*' Thomas 1884 : 17; pl. 1, fig. 9). The holotype of *G. thomasi* is a right horn core base, mistakenly shown as a left in Thomas's illustration, which is very small and possibly from a young animal. Its basal anteroposterior and mediolateral diameters are 21·2 × 14·7 mm. It thus shows strong mediolateral compression like the Omo *G. praethomsoni*, as was discussed by Arambourg (1947 : 389–390). *G. setifensis* is larger, and is less compressed and more curved.

Plate 40 (Scale = 50 mm for Figs 1–5 and 25 mm for Fig. 6)

Fig. 1 **Alcelaphini** sp. 3. Anterior view of left horn core, SHK II 1953.280.

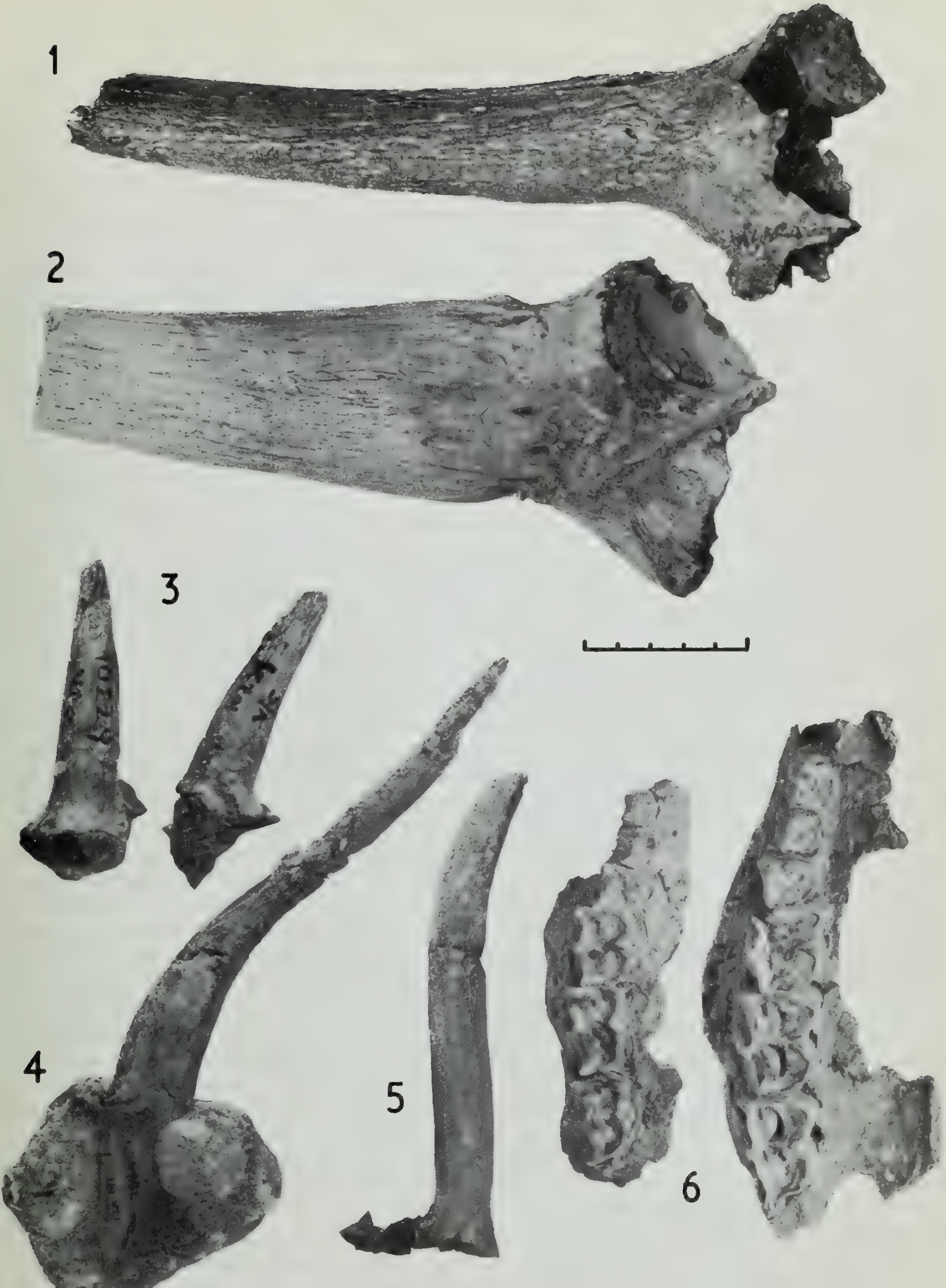
Fig. 2 **Alcelaphini** sp. 3. Lateral view of right horn core, F 3000.

Fig. 3 ? **Neotragini** indet. Two views of horn core, FLKN I 10229.

Fig. 4 **Alcelaphini** sp. 4. Horn core, FLKN I 7884.

Fig. 5 **Alcelaphini** sp. 4. Horn core, FLKN I 5196.

Fig. 6 ***Antidorcas recki***. Right P^2–M^3 of FLKN I 1152 (on the left) and of FLKN I 1662 (on the right).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2
3
4
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6

Its basal anteroposterior and mediolateral diameters are given as 38 and 24 mm, which is larger than in the Olduvai gazelle.

One of the three gazelles from Laetolil named by Dietrich may be close to the Olduvai gazelle despite the greater antiquity of the Laetolil fauna. There are four right and six left nearly complete horn cores in Berlin of *G. janenschi* Dietrich (1950 : 25; pl. 2, fig. 22) from the Vogel River, Gadjingero, Deturi and Garussi water courses. The illustrated left horn core from Garussi is almost complete and has preserved the supraorbital pit, midfrontal and parietofrontal sutures. The horn core is moderately long, very little compressed, inserted obliquely and close to the midfrontal suture, curves a little backwards and lacks a flattened lateral surface, keels or transverse ridges. In anterior view its slight outward divergence lessens towards the very tip. It has deep longitudinal grooving posteriorly, a deep and localized postcornual fossa, and there is extremely little hollowing of the frontals. The specimen can be eliminated from the Reduncini by the narrow and rather drawn-out triangular supraorbital pit, and in any case small reduncine teeth are lacking in all Laetolil collections.

Horn cores similar to those of *G. janenschi* in the London Laetolil collection are an almost complete left horn core BM(NH) M 22483, incomplete right horn core M 22493, basal half of left horn core M 22491, and parts of horn cores M 22494 and M 22484. In Nairobi are the bases of left horn cores 1959.46 and 1959.50, bases of right horn cores 1959.48 and 1959.49, and the basal half of a right horn core MUG (Mugheim) 1, of which 1959.49 and 1959.50 are the best preserved. The crushed skull in Berlin (Dietrich 1950 : pl. 5, fig. 52) is probably a female of *G. janenschi* as Dietrich suggested. It has extremely worn teeth. BM(NH) M 22491 and M 22493, and 1959.49 and 1959.50 in Nairobi, have more internal hollowing of the frontals, more flattening of the lateral surface, and perhaps greater initial divergence than in the other specimens.

G. janenschi differs from the Olduvai gazelle in having horn cores less thickened at the base, divergence lessening slightly towards the tip, no flattening of the lateral surface and more backwards curvature. In the absence of any contrary evidence, it is possible that *G. janenschi* could be ancestral to the Olduvai, Peninj and Elandsfontein gazelle.

There seems little reason to separate the maxillae assigned by Dietrich to '*Gazella hennigi*' (1950 : pl. 5, fig. 47) from the teeth and mandibles assigned to *G. janenschi* (pl. 2, figs 14–15; pl. 5, fig. 48); the *G. janenschi* 'maxillae' of pl. 5, fig. 48 are single teeth, on the large side, which have been mounted together in plaster. Such teeth and dentitions are smaller than those of *Antidorcas recki*. Similar antilopine teeth and dentitions are in the London Laetolil collection. These are partial left mandibles BM(NH) M 15110 and two numbered M 22488, two right mandibles numbered M 22486 and two numbered M 22487, right M_3 in fragment of mandible M 26784, right $M^1 + P^4$ M 22485, left upper molars M 22485, M 22495 and one without number. Comparable remains in Nairobi are a complete left lower dentition 1959.603 + 605, partial left lower dentition 1959.143, partial right lower dentitions 1959.152 and 1959.296 + 298, right maxilla with two molars 1959.452, right upper molars 1959.308, 1959.319, 1959.320 and 1964. no number, left upper molar 1959.321, and four right lower molars without number found in 1959. The mandibles in London all show that the ramus below the teeth is shallow, as in the Olduvai *Gazella* mandibles SHK II 1957.793 and BK II 1952.152, and the M_3s have enlarged back lobes.

Two incomplete Laetolil left mandibular pieces have rami too deep for them to belong with the other specimens. They are 1959.54 in Nairobi which is in two parts with M_2 and M_3 on one part and P_2 and P_3 on the other, and M 29428 in London with the back of deciduous P_4, M_1 and M_2. The P_2 of 1959.54 is very small. Possibly these fossils represent *Antidorcas*.

The teeth assigned to *Gazella kohllarseni* by Dietrich (1950 : 25; pl. 2, fig. 16; pl. 5, fig. 49), all three 'tooth rows' consisting of single teeth mounted in plaster, appear antilopine, are larger than the teeth of *G. janenschi* and must belong to another species. Similar remains are present among the London Laetolil material (e.g. partial left mandible M 22487 and a left lower molar M 22488) and in Nairobi (incomplete left mandibles 1959.150, 1959.294 and 1959.443 + 444, left lower molar 1959.168, left upper molar 1959.315 and right upper molar 1959.625). These fossils are the same size as or still larger than the large antilopine maxilla 1662 from Olduvai FLKN I and some single teeth from FLK I and FLKN I. Some of them may belong to relatively recently fossilized *G. granti* (see p. 293).

The left horn core from Garussi called *G. kohllarseni* by Dietrich (1950 : 25; pl. 1, fig. 7) is unlikely to belong in the Antilopini (see p. 351).

A left horn core BM(NH) M 15883 from Kanam West, with basal diameters of 32·2 and 22·8 mm, is larger than the Olduvai gazelle but agrees in the rather anterior level of the maximum mediolateral diameter.

A fuller picture of the evolution of gazelles in Africa south of the Sahara can only emerge from the finding of much more complete specimens than we have at present. It is very doubtful if one can get a reliable story by considering only the degree of mediolateral compression of the horn cores. The conclusions which can be made at present about gazelles are as follows. African fossil gazelles are known back to the late Miocene (Gentry 1970a : 293). Their range has extended at times to the southernmost tip of the continent, although nowadays they go no further south than Tanzania. The Olduvai gazelle from middle and upper Bed II is conspecific with the gazelle at Elandsfontein; it could well have been the ancestor of the extant *G. thomsoni* and *G. rufifrons*, and may itself be descended from the Laetolil *G. janenschi*. The Omo *G. praethomsoni* is different from the Olduvai middle and upper Bed II gazelle and may represent a different lineage. It may not be different from some of the supposedly earlier Olduvai horn cores, especially BM(NH) M 14508, which are only provisionally considered conspecific with the later Olduvai ones. There is more definite evidence for a second lineage of gazelles which will be considered under the next heading.

Fossil remains of larger gazelles

Schwarz (1937 : 53; pl. 2, figs 6–7) referred to *Gazella granti* a radius, two ulnae and three metatarsals from Olduvai, but this material has not survived the Second World War. One of the ulnae and the radius were illustrated, but the photographs do not show any characters whereby the bones can be identified. Therefore we have not included *G. granti* on the Olduvai list.

The base of a right horn core of *G. granti*, 1959.236, is present in the Laetolil collection at Nairobi. It is less mineralized than other Laetolil fossils, and is most likely to be of late Pleistocene or Recent age. Dietrich (1950 : 27) also referred to *G. granti* in the younger deposits at Laetolil. Pieces of a probable right horn core BM(NH) M 15851 + M 25627 and a left one M 15851 from Kanjera could belong to *G. granti*. M 15883 from Kanam is smaller but similar.

The horn core from Karungu M 22502 said by Gentry (1966 : 104) to resemble *G. granti* now looks to us more like a Recent and scarcely fossilized *G. thomsoni*.

The remains of a large gazelle from Makapansgat Limeworks were first described by Wells & Cooke (1956 : 43, figs 22–24) as *Phenacotragus vanhoepeni* but have now been correctly referred to *Gazella* by Wells (1969b : 162). The horn cores of this species are moderately long, strongly compressed with a flattened lateral surface, without keels or transverse ridges, inserted rather uprightly above the orbits and moderately far apart. They bend sharply backwards half-way along their length and are nearly parallel except for slightly increased divergence towards their tips. Some features seen on the crania are the rather wide orbital rims, small to moderate preorbital fossae, only a slight central indentation of the parietofrontals' suture, a prominent median occipital ridge with poor flanking hollows, large mastoids, fairly large auditory bullae, small foramina ovalia and little transverse constriction on the basioccipital.

Wells (1969b : 162) has already mentioned that *G. vanhoepeni* could belong with the group of large living gazelles comprising *G. granti*, *G. soemmerringi* and *G. dama*. Indeed in several characters it is plausible as an ancestor for *G. granti*; these are the uprightly inserted and mediolaterally compressed horn cores, a fairly long braincase, deep postcornual fossae, a complicated and raised midfrontals suture, moderate-sized but not large supraorbital pits and large anterior tuberosities of the basioccipital.

G. gracilior from Makapansgat Limeworks is probably conspecific with *G. vanhoepeni* as discussed previously on p. 440. The horn cores assigned to this name are likely to be the females of *G. vanhoepeni*, and they are a little bigger relative to those of the males than in living gazelles. *G. vanhoepeni* would therefore be characterized by rather poor sexual dimorphism of its horns.

Vrba (1973 : 309 footnote) has made the tentative suggestion that *G. gracilior* may turn out to be an *Antidorcas*, but we prefer to maintain our existing opinion.

Gazelle horn cores from Langebaanweg (L.3491, L.6077, L.6078, L.9149 and L.10694) are mediolaterally compressed and curve backwards quite strongly. They are large for their geological age (Pliocene), and could be ancestral to *G. vanhoepeni.*

Genus **INDETERMINATE**

Antilopini sp. 1

A number of small horn cores from Olduvai can perhaps be placed in the Antilopini. These are

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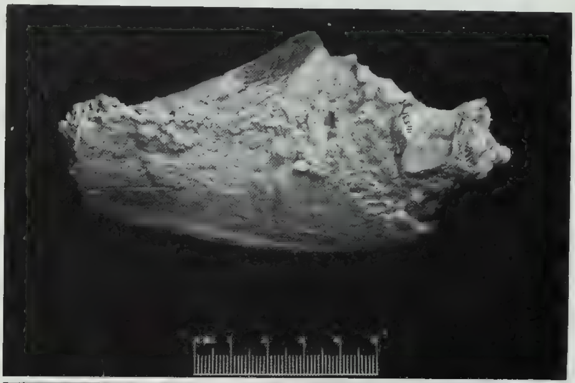

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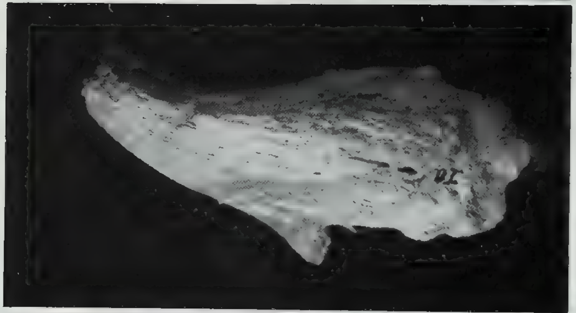

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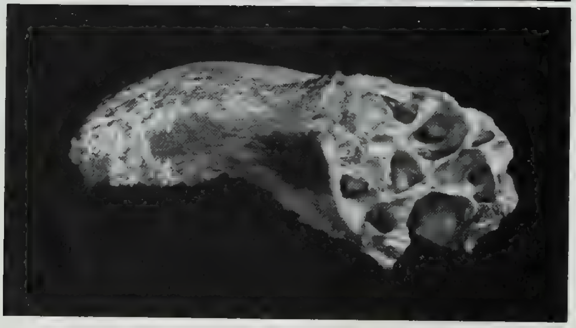

Plate 41 (Scale marked in cm and mm)

? Caprinae sp.

Fig. 1 Supposed dorsal view of right horn core from Bed I, BM(NH) M 14531.

Fig. 2 Supposed anterior view of same horn core.

Fig. 3 Supposed posterior view of same horn core.

the basal half of a left horn core with the midfrontal suture and supraorbital pit 1962.067/3963 (Pl. 39, fig. 2) and the basal part of a left horn core 1962.067/3965, both from the surface of DK I, the basal part of a left horn core with the midfrontal suture and supraorbital pit MNK II 1963 .2818, the basal part of a left horn core with the midfrontal suture, supraorbital pit and top of the orbital rim BK II 1955.63, the base of a right horn core BK II 1957.991, and the basal part of a left horn core BM(NH) M 22364. The horn cores are a little compressed mediolaterally, without a flattened lateral surface, with a slight approach to a posterolateral keel, inserted on short pedicels above the orbits, inserted fairly uprightly in side view, almost parallel at the very base in front view but with rapidly increasing divergence above, with a small and moderately deep postcornual fossa, no internal hollowing of the frontals, frontals between the horn core bases not raised above the level of the top of the orbital rims, and fairly large triangular supraorbital pits.

Most of these characters would fit *Gazella* very well, but the lack of any flattening of the lateral surface, the more upright insertions, and the rapidly increasing divergence above the base are differences from the other gazelle horn cores from Olduvai. Moreover the definite Olduvai *Gazella* is represented at BK II alongside this species, and appears to be no different in size. If both species are really antilopine, perhaps one was comparable in way of life to the living *Litocranius walleri*. One might wonder about uniting this species with Alcelaphini sp. 4, but at present it still seems that the latter is distinguished in its internally hollowed horn core pedicel, slightly greater mediolateral compression, and stronger spiralling. It is also likely to be an earlier species than Antilopini sp. 1.

Measurements. Anteroposterior and mediolateral diameters at the base of these horn cores are:

DK I 1962.067/3963	27·6 × 24·2	BK II 1957.991	28·4 × 22·6
MNK II 1963.2818	31·7 × 24·0	BM(NH) M 22364	25·7 × 20·0
BK II 1955.63	31·4 × 24·9		

Comparisons. Three horn cores from the Shungura Formation at Omo, F203-32 and F203-103 from member K and F356-10a from member L, appear conspecific with the Olduvai horn cores.

Subfamily **CAPRINAE**

This is basically a Eurasian subfamily, living members of which occur also in North America and on the fringes of the Palaearctic faunal realm in Africa. Two early African bovids from Fort Ternan have been assigned to the Caprinae (Gentry 1970a : 262, 284) on the basis of their very close resemblance to their Eurasian contemporaries. There is slender evidence for supposing that later members of these lineages evolved into Alcelaphini (Gentry 1970a : 315), and that living Caprinae and their fossil relatives evolved in Eurasia (Gentry 1971). However, it is now known that at least one (Gentry 1970b) and probably two species of the caprine tribe Ovibovini have in the past inhabited regions of Africa remote from the Palaearctic.

Makapania broomi Wells & Cooke (1956 : 26) from Makapansgat Limeworks has been assigned by Gentry (1970b) to the Ovibovini, and appears to be very similar to the European Villafranchian *Megalovis latifrons* Schaub.

It also seems likely that a second ovibovine lineage has inhabited Africa. BM(NH) M 14531 (Pl. 41) is a small horn core with part of the frontal found in Olduvai Bed I in 1932. It tapers quickly from a wide compressed base, and curves in two planes. There are no keels or transverse ridges. A small surface concavity can be seen on what is likely to be the ventral side. Part of the frontal's surface medial to the horn core base seems to lie on the vertical plane and must certainly be at an angle to the rest of the skull roof. The broken frontal shows an extensive system of small sinuses quite unlike the large sinuses of Alcelaphini, but similar to those which occur in Ovibovini and Bovini. The plane of the frontals shows that the horn core cannot be from a small *Syncerus*. This rather mysterious horn core shows some resemblance to the frontlet of '*Bos*' *makapaani* Broom (1937 : 510, figured) described from a cave 'near Makapaansgat, about 10 miles from Pietpotgieters Rust' which later became known as Buffalo Cave (Cooke 1952 : 33). There is reason to suppose, from the likely position of the sutures, that the convex edges of the horn cores on Broom's frontlet are anterior or anterodorsal and not posterior. This would give it some resemblance to *Budorcas taxicolor* Hodgson, the living takin of Tibet and western China. Possible ovibovine remains also occur at other sites, for example three teeth in members C, D and G of the Shungura Formation, Omo.

Three caprine-like metapodials have also been excavated from Bed I. A right metatarsal 067/1009 from FLKN I level 3, a left metatarsal 068/6665 from levels 1-3, and a left metacarpal 9394 from level 5 which was referred to the Caprini by Leakey (1965 : 68(a)), are complete and are very short (Pl. 19, fig. 2). The metatarsal 068/6665 has low distal condyles with outside edges not parallel and poor distal flanges on the anterior surface. However, it cannot be tragelaphine because the rear naviculocuboid facet is strongly pointed upwards at the back. The anterior central groove is not markedly deep, but the hollows flanking the distal condyles are deep. The posterior surface is not hollowed. The second metatarsal is slightly longer and thinner. Measurements of length and least thickness on these metatarsals are:

FLKN I 068/6665	167 × 23·8	FLKN I 067/1009	173 × 20·2

The metacarpal has a magnum–trapezoid facet which lacks a protuberance on its medial side. The unciform facet is relatively larger than in Alcelaphini, and it has no posterolateral projection nor an anterolateral angled edge. This limb bone measures 175 × 24·9 mm.

The distal ends of these metapodials are rather like small Bovini but the proximal ends are not. They are similar to goats in the rather poor distal flanges on the anterior surface, the not very upcurved ectocuneiform facet in side view, the longitudinal groove on the metatarsal front, the anteroposterior compression of the whole bone, the shortness and the low distal condyles.

The distal end of a left tibia FLKN I 7243 from levels 1–2 may belong with the metapodials. The posterior edge of the articular facet is very little indented centrally and the size would agree with the metapodials.

Continued in Part II, published as *Bull. Br. Mus. nat. Hist.* (Geol.) **30** (1).

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